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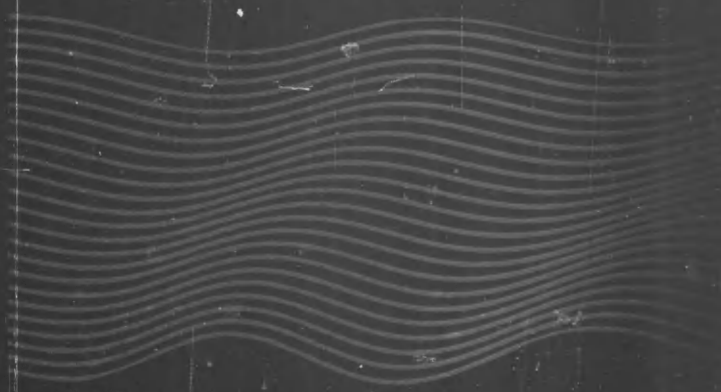
Journal canadien des sciences halieutiques et aquatiques



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Statistical Power Analysis can Improve Fisheries Research and Management[1]

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Peterman, R. M. 1990. Statistical power analysis can improve fisheries research and management. Can. J. Fish. Aquat. Sci. 47: 2–15.

Ninety-eight percent of recently surveyed papers in fisheries and aquatic sciences that did not reject some null hypothesis (H_0) failed to report β, the probability of making a type II error (not rejecting H_0 when it should have been), or statistical power ($1-\beta$). However, 52% of those papers drew conclusions as if H_0 were true. A false H_0 could have been missed because of a low-power experiment, caused by small sample size or large sampling variability. Costs of type II errors can be large (for example, for cases that fail to detect harmful effects of some industrial effluent or a significant effect of fishing on stock depletion). Past statistical power analyses show that abundance estimation techniques usually have high β and that only large effects are detectable. I review relationships among β, power, detectable effect size, sample size, and sampling variability. I show how statistical power analysis can help interpret past results and improve designs of future experiments, impact assessments, and management regulations. I make recommendations for researchers and decision makers, including routine application of power analysis, more cautious management, and reversal of the burden of proof to put it on industry, not management agencies.

Quatre-vingt-dix-huit pour cent des articles publiés sur les sciences halieutiques et aquatiques récemment examinés qui ne rejettent pas l'hypothèse nulle présentée (H_0) ne font pas état de β, la probabilité d'une erreur de type II (l'acceptation erronée de H_0) ou du facteur de puissance statistique $1-\beta$. Toutefois, 52 % de ces articles présentent des conclusions basées sur une H_0 véritable. Il est possible qu'une H_0 erronée n'ait pas été identifiée à cause d'une expérience à faible facteur de puissance résultant d'une petite taille d'échantillon ou d'une forte variabilité de l'échantillonnage. Les coûts d'erreurs de type II peuvent être importants, par exemple dans les cas où les incidents nocives d'eaux résiduaires industrielles ou l'appauvrissement par pêche d'un stock ne sont pas relevés. Des analyses du facteur de puissance statistique antérieures révèlent que les méthodes d'estimation de l'abondance ont un β élevé et que seules les importantes incidences sont relevées. L'auteur examine la relation entre β, la puissance, la magnitude de l'incidence décelable, la taille de l'échantillon et la variabilité de l'échantillonnage. Il montre comment l'analyse du facteur de puissance statistique peut servir à l'interprétation de résultats d'expériences passées et à l'amélioration de la conception d'expériences futures, d'évaluations des incidences environnementales et de normes de gestion. Il présente des recommandations à l'intention des chercheurs et des preneurs de décisions, y compris l'application routinière d'analyses de puissance, pour une gestion plus prudente et le renversement des rôles en ce qui concerne le fardeau de la preuve, qui devrait relever des industriels et non des organismes de gestion.

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Most fisheries and aquatic scientists quite properly follow the tradition of Platt (1964) and Popper (1968); they structure their research around formal tests of null hypotheses. For example, data are frequently used to test a null hypothesis (H_0) such as, (1) "there is no relationship between recruitment in a fish population and some oceanographic variable," or (2) "there is no effect of a pollutant on mortality rate," or (3) "fish abundance is not changing." Most scientists report the cases in which they *reject* an H_0 at some level of significance, α. However, they generally do not apply the equally important concept of statistical power to interpreting cases where they *fail to reject* some H_0, and in many of those cases they draw unjustified conclusions (Toft and Shea 1983; Hayes 1987).

Problems can arise if researchers or resource managers conclude that H_0 is true when it is not rejected. Such workers might conclude, for example, that fish recruitment is not affected by upwelling, or that a hatchery is not increasing adult abundance. If indeed there was no effect, such conclusions would be correct. However, it is also possible that a real effect existed in nature but that no significant relationship was found because of large sampling variability or small sample size. Clearly, it would be useful to have more information on these alternatives, and that is exactly what statistical power analysis provides.

Statistical power is a well developed concept that can be used to strengthen inferences drawn from fisheries research. It also has importance implications for management of fisheries and other natural resources. Suppose, for example, that some past experiment failed to show a significant effect of pulp mill effluent on fish mortality rate. Statistical power analysis could show managers the magnitude of effect that could have been detected by the experimental design. Similarly, it could provide managers with the probability that a 40% decline in fish stock abundance could be detected with current types of data. In these examples, if managers knew that only very large effects could have been detected or that there was only a low probability of detecting a decrease in abundance, their decisions might well be different than ones made in the absence of such information. Unfortunately, scientists rarely calculate such detectable effect sizes or probabilities of detection, let alone provide them to managers (Toft and Shea 1983; Hayes 1987). However, methods to calculate these quantities are widely available (Dixon and Massey 1969; Winer 1971; Pearson and Hartley 1976; Muller and Peterson 1984; Kraemer and Thiemann 1987; Cohen 1988). This information is a useful addition to that available from standard reporting of *P* values and confidence intervals.

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[1] J. C. Stevenson Memorial Lecture, delivered 3 January 1990, Ottawa, Ontario.

The purpose of this paper is to review statistical power concepts for those who design data gathering programs, perform and interpret statistical analyses of biological data, or use the results of such analyses. The audience thus includes research biologists and scientists, consultants, managers, decision makers, and policy makers. Many of the examples that I use focus on fisheries management. However, all readers, regardless of their speciality, will probably find the ideas in this paper relevant because statistical power analysis is useful wherever statistics are used to test hypotheses, including biological research, impact assessment, and resource management (e.g. Toft and Shea 1983; Hayes 1987; Millard 1987).

Graphical Overview of Statistics

To clarify the notion of statistical power, it is necessary to review some basic statistical concepts with a very simple example. The review below explains graphically how statistical power fits into common scientific statistical practices.

The Canadian Department of Health and Welfare has set 2 mg/kg of fish as the maximum tolerance level for polychlorinated biphenyls (PCBs) in edible portions of fish in the Great Lakes (Sonzogni and Swain 1984). Suppose that you take a sample of 30 fish to determine whether the mean PCB concentration, $\bar{X}$, is significantly greater than 2 mg/kg. Your null hypothesis is that the mean PCB concentration meets the health standard, in other words that the true mean value in the fish population, μ, is ≤ 2, i.e. H_0: $\mu \leq 2$. The alternative hypothesis (H_A) is that PCBs exceed the health standard, i.e. H_A: $\mu > 2$. Suppose that to test the H_0, you use a one-sample, one-tailed *t*-test. If statistical analysis of the data leads to rejection of H_0, then you accept H_A. To clarify discussions, I have deliberately chosen a simple example (with a one-tailed, one-sample *t*-test) but the concepts outlined below are generally applicable.

Table 1 illustrates the four possible outcomes of the hypothesis test, depending on the true "state of nature." If you *reject* the null hypothesis that the PCB concentration meets the health standard, and if in reality, this null hypothesis is actually true, then you will make a type I error (box 2 of Table 1). However, if the PCB concentration actually exceeds the health standard (i.e. if the null hypothesis is actually false in nature), then you will draw the correct conclusion by rejecting H_0 (box 4 of Table 1). Similarly, two outcomes are possible if you do not reject the null hypothesis. If H_0 is actually true, you will draw the correct conclusion (box 1), but if H_0 is actually false, you will make a Type II error (box 3).

Sampling Distributions

To simplify this example further, I will take a special case of the general null hypothesis, H_0: $\mu \leq 2$, specifically, that the true population's mean PCB concentration in fish, μ, is 2 mg/kg, i.e. H_0: $\mu = 2$. This is the most relevant special case because 2 mg/kg is the upper limit to the legally acceptable range of PCBs. If this H_0: $\mu = 2$ is true, then the PCB concentration meets the health standard, albeit barely. With your sampling and measurement methods, suppose that you have a sample variance $s^2 = 0.36$. *If H_0 is true* (i.e. $\mu = 2$), then you would expect the sampling distribution of observed $\bar{X}$ values obtained from a large number of samples of 30 fish each to appear as in Fig. 1A. As usual, you set an acceptable α level of significance (say 0.05), which specifies the probability of type I error (Table 1) that you are willing to tolerate. α also defines a critical value for $\bar{X}$ (in this case 2.19 mg/kg, the vertical dashed line in Fig. 1), beyond which you reject H_0, but to the left of which you do not reject H_0. In other words, the top sampling distribution shows the probability of obtaining various $\bar{X}$ values by chance alone, *if H_0 were true*. Because this paragraph discusses the case in which the H_0 is true in nature, the outcomes of rejecting or not rejecting the null hypothesis are boxes 2 and 1 in Table 1, respectively.

However, now consider the case in which the null hypothesis is actually false in nature and that, for example, $\mu = 2.1$ in the true population. In this case, the sampling distribution $\bar{X}$ values would have a mean of 2.1, and to determine what would happen in this situation, examine only Fig. 1B. If the sample mean $\bar{X}$ exceeds the critical value of 2.19 (which would occur 5% of the time if H_0:$\mu = 2$ were true), then you reject H_0. If you reject H_0 in this case, you will do so correctly (box 4 of Table 1) because the true $\mu = 2.1$. However, if the observed $\bar{X}$ is to the left of the critical value of 2.19, you will fail to reject the null hypothesis, but this will be incorrect. That is, you will incorrectly conclude that $\mu = 2$, when in fact the observed $\bar{X}$ came from the sampling distribution in Fig. 1B in which the true $\mu = 2.1$. This gives rise to a type II error (box 3 of Table 1).

Suppose that in your sample, $\bar{X}$ turned out to be 2.1, which gives $P > 0.18$. You would thus not reject the H_0 because $P > \alpha$, and you would probably conclude that there is no need to take action against manufacturers or users of PCBs. However, with a true population $\mu = 2.1$, there is a very high probability that

TABLE 1. Four possible outcomes (referred to in the text by box numbers) for a statistical test of some null hypothesis, depending on the true state of nature. The probability for each outcome is given in parentheses. Adapted from Toft and Shea (1983).

	Decision	
State of nature	Do not reject null hypothesis	Reject null hypothesis
Null hypothesis actually true	1. Correct $(1-\alpha)$	2. Type I error (α)
Null hypothesis actually false	3. Type II error (β)	4. Correct $(1-\beta)$ (=power)

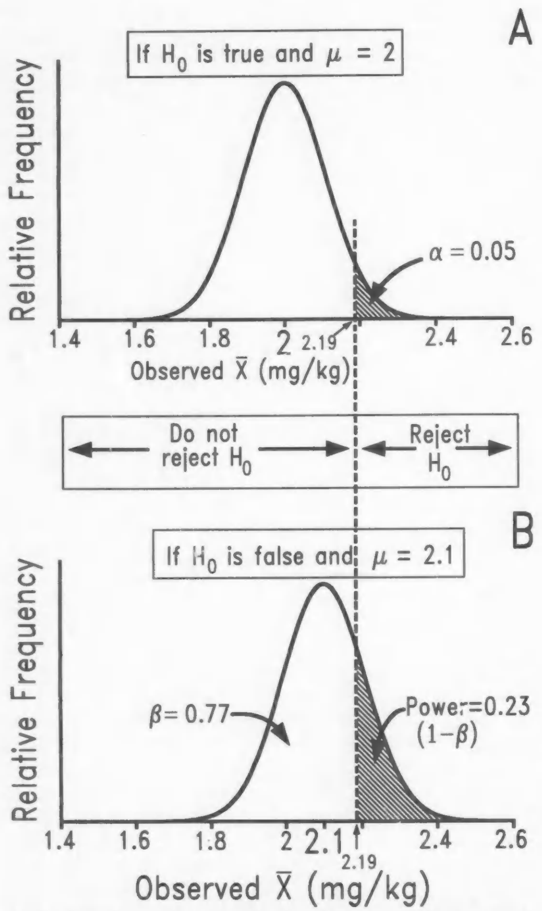

FIG. 1. Example sampling distributions for mean PCB concentration in samples of 30 fish. Part A is the sampling distribution for the case in which the null hypothesis, H_0, is true and the true population mean PCB concentration, μ = 2 mg/kg, with $s^2=0.36$. The shaded area in part A is the critical region for $\alpha=0.05$ and the vertical dashed line is at the critical $\bar{X}$, 2.19. Part B is the sampling distribution for the case in which the H_0 is false and $\mu=2.1$ mg/kg. In both distributions, a sample $\bar{X}$ to the right of the vertical dashed line would reject H_0, and to the left of it, would not reject H_0. Power and β values in part B, in which H_0 is false and $\mu=2.1$, are the proportion of $\bar{X}$s that would occur in the regions in which H_0 was rejected or not rejected, respectively.

you would not reject the null hypothesis even though it is false, as shown by the unshaded area under the distribution in Fig. 1B to the left of the critical value of 2.19. This area is β, which is the probability of making a type II error. As shown in Fig. 1B, even if the true $\mu=2.1$, there is still a 77% chance that you will not reject the H_0, perhaps because of the sample variance or small sample size. Hence, without knowing this probability of making a type II error, you may *unjustifiably* conclude that there is no problem with PCBs when in fact the health standard has been exceeded (i.e. $\mu=2.1$, not 2).

Statistical Power

Statistical power is defined as $1-\beta$, where β is the probability of failing to reject the H_0 when in fact H_0 is false. Power thus reflects the probability of correctly rejecting H_0 (shaded area of Fig. 1B and Dixon and Massey 1969), e.g. rejecting the H_0 of no problem with PCBs when in reality PCB concentration is above the acceptable level.

A major point of this paper is that statistical power concepts should be applied regularly by fisheries scientists, but they are not. Most fisheries scientists emphasize the importance of type I error by setting $\alpha=0.05$ and reporting P values associated with it, while paying little attention to type II errors and the power of their tests (their ability to avoid type II error). They fail to recognize that type II errors in fisheries (caused by using tests or experimental designs with low power) can often be more serious than type I errors (Toft and Shea 1983). Ignorance of type II errors is especially dangerous when a statistical analysis does not reject the null hypothesis and when the analyst recommends action based on the conclusion that H_0 is true. This de facto assertion that H_0 is true, even though results show only that H_0 has not been falsified, is a logical jump that scientists and resource managers often make. However, the conclusion that H_0 is true is not justified unless the analyst shows that β, the probability of making a type II error, is sufficiently low. "Sufficiently low" differs among people and situations but in general one would like β at least <0.2, or power >0.8. If one wants to be as conservative about making type II as type I errors, set $\beta=\alpha$, or desired power$=0.95$ for $\alpha=0.05$.

In this paper, I purposely avoid using the terminology "accept the null hypothesis," and instead refer to "not rejecting H_0" or "failing to reject H_0." This is to emphasize the important point that proper resource management depends on a two-step process. First, a statistical analysis will either reject the H_0 or not. Second, β or detectable effect size (to be described later) must be calculated if H_0 is *not* rejected. Decision makers should take action based on the assumption that the H_0 is true *only if* the probability of making a type II error is acceptably low. As explained later, a major problem has been that decision makers have taken action without going through the second step, i.e. they have "accepted" the null hypothesis as true after going through only the first of the above steps and failing to reject H_0.

Ideally, experiments or field data sets should have high power or a high probability of detecting an effect (e.g. of oceanographic conditions, density, fishing, etc.) if an effect exists (i.e. rejecting H_0 if it is not true). Unfortunately, most papers in fisheries research in which the H_0 is asserted to be true, either explicitly or implicitly, do not even report power or β, let alone show that they are within acceptable ranges (and I even admit making this mistake myself in the past, e.g. Peterman 1982). A survey of recent publications in two fisheries journals documents the above contention (Table 2). Of 408 papers read, 160 reported at least one case of a failure to reject an H_0. Eighty-three papers made a total of 142 recommendations or interpretations as if the H_0 had been shown to be true, yet only *one* of those 142 cases (Morin et al. 1988) calculated the probability of making a type II error (failing to reject H_0 even though H_0 was false)! Only two other papers (Arnason and Mills 1987; Parkinson et al. 1988) even mentioned power in any context, and these papers dealt with estimating power for various hypothetical situations that experimenters might encounter in the future. While this literature search is not exhaustive, it is probably representative of the current situation. Thus, the problem that I address is widespread in the fisheries and aquatic sciences, yet its solution is fairly straightforward, as I show below.

Several factors influence power. In general,

TABLE 2. Results of a literature survey to determine the number of (1) papers that failed to reject a null hypothesis, H_0, because P exceeded α (usually 0.05); (2) papers that asserted that an H_0 of no effect was true; (3) different assertions of no effect (some papers made more than one such assertion); and (4) papers that reported either β, the probability of failing to reject the H_0 when in fact H_0 was false, or power $(1-\beta)$. Issues of the Canadian Journal of Fisheries and Aquatic Sciences searched were chosen randomly from 1987, 1988, 1989: volumes 44(1, Suppl. 1, Suppl. 2, 12), 45(3, 4, 8, 10, 12), and 46(4). Issues searched of the North American Journal of Fisheries Management were those available to us for 1987 and 1988: volumes 7(1, 2, 3, 4) and 8(1, 2, 3).

Journal searched	Number of papers searched	Number of papers with at least one occurrence of not rejecting a null hypothesis	Number of papers with at least one assertion of no effect	Number of assertions of no effect	Number of papers that reported β or power
Canadian Journal of Fisheries and Aquatic Sciences	257	111	59	87	2
North American Journal of Fisheries Management	151	49	24	55	1
Totals	408	160	83	142	3

(1) Power = some function of (α, effect size, N, and s^2),

where α is the stated value for P (the calculated probability) below which you reject H_0, effect size is the magnitude of the true effect for which you are testing, N is the sample size, and s^2 is the sample variance. Often, the latter two terms are combined into a measure of the reliabilty of sample results (Toft and Shea 1983; Cohen 1988). Note that s^2 includes both natural variability in the sampled parameter as well as measurement error. In the PCB example above, effect size is related to the difference between the true parameter value and its value if the H_0 were true (e.g. 2.1–2.0). Power is also affected by the degree to which the data fail to meet the statistical method's assumptions. However, I will not discuss this latter point because failures to meet such assumptions can create biases as well as errors that are specific to each statistical method; these are beyond the scope of this paper.

Specific forms of equation (1) are available to calculate power, depending on the particular statistical method being used (t-test, ANOVA, etc.) (Dixon and Massey 1969; Winer 1971; Pearson and Hartley 1976; Cohen 1988). The general effect of each factor in equation (1) on power is shown graphically in Figs. 2 to 4, holding all other factors constant in turn.

First, power is positively related to α. If, for example, the scientist investigating mean PCB concentration decides to be more stringent with respect to type I errors and decreases α to 0.01 from its conventional 0.05 (black shading on right edge of Fig. 2A), power will decrease to 0.07 (Fig. 2B) from 0.23 in Fig. 1B, and the probability of making a type II error, β, will therefore increase to 0.93 from 0.77 in Fig. 1B. However, if $\alpha = 0.10$ is tolerable, then power will increase to 0.35 (black plus grey area, Fig. 2B).

Second, larger effect sizes have higher power than small effect sizes because the distance between the means of the true sampling distribution and the null distribution is larger (Fig. 3). Hence, if you repeat your sample of 30 fish at some later date when the true $\mu = 2.2$ or even 2.3 mg/kg (Figs. 3B and 3C), then the rejection regions in these lower panels, as defined by the stated α in Fig. 3A, will be larger than in Fig. 1B. With $\mu = 2.2$ or 2.3, power will be 0.56 and 0.84, respectively, instead of 0.23 when $\mu = 2.1$. Thus, experiments with large perturbations or effects are more likely to generate high power, i.e. high probability of obtaining a statistically significant result. This point is worth emphasizing; power can only be calculated with respect to a specific alternative parametric value, although a set of possible values can be explored. The closer the parametric value is to the null hypothesis, the lower the power and the harder it will be to find a statistically significant result.

Third, power is also positively related to the reliability of samples. Given a stated α, narrower null and alternative distributions cause the critical value of $\overline{X}$ that leads to rejection of H_0 to approach the null hypothesis value of 2, thereby shifting the vertical dashed line closer to 2 (cf. critical values in Figs. 4A and 1A). The distribution in Fig. 4B also narrows but power increases as the vertical dashed line shifts to the left. In Fig. 4B, with sample variance $s^2 = 0.0625$ instead of 0.36, power is 0.69 instead of 0.23. The distributions can be made narrower by changing to a more precise method of measurement or increasing the sample size; to give the same distribution as in Fig. 4B with s^2 remaining at the original 0.36, sample size could be increased to 173 from 30.

Types of Power Analysis

It is helpful to identify different types of power analysis in fisheries before giving detailed examples. First, statistical power analysis can be done before the start of data collection programs, experiments, or management manipulations (a priori analysis), or after their completion (a posteriori analysis). Second, analysts can go well beyond simply estimating power for a given situation. By rearranging the appropriate specific form of equation (1), they can solve for any one of its terms, if the rest are known or can be assumed. For example, if an analyst can state α, s^2, and an assumed effect size, the sample size required to achieve a desired power can be calculated. This can be repeated for different assumed effect sizes. Similarly, if α, the sample size, and s^2 are known, one can solve for the "detectable effect size," the effect size that would have to exist to give a desired power. This use of the term "detectable" is very specific in power analysis. A detectable effect in a certain experimental design yields a probability of rejecting H_0, if H_0 is false, greater than or equal to the stated desired power. For instance, in experimental design work, one may want to find the sample size required to make the phenomenon detectable in the sense that there will be a 90% chance (or some other

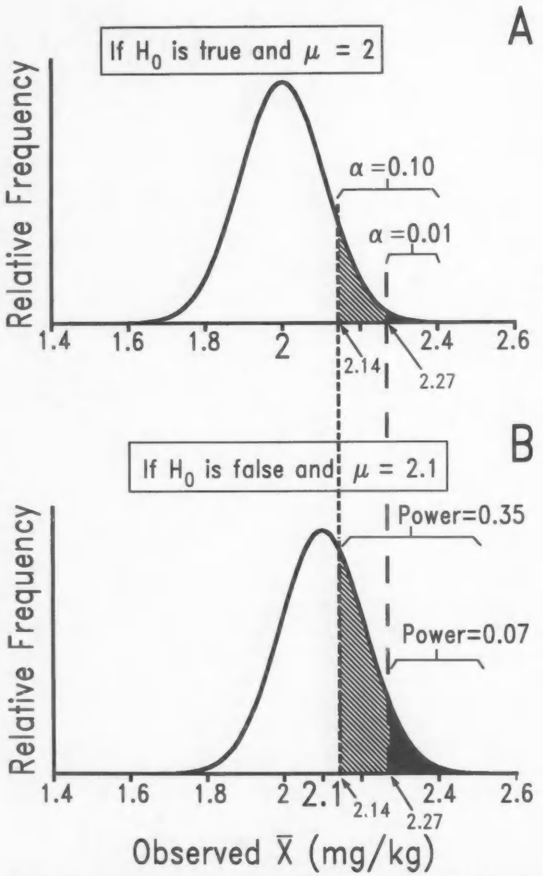

FIG. 2. Same as Fig. 1 except two critical regions are defined in part A, for $\alpha = 0.01$ and $\alpha = 0.10$. The critical region for $\alpha = 0.10$ overlaps that of $\alpha = 0.01$. Part B, in which the H_0 is false and $\mu = 2.1$, shows that power (the probability of correctly rejecting H_0) is larger for the $\alpha = 0.10$ case and smaller for the $\alpha = 0.01$ case than for Fig. 1 where $\alpha = 0.05$.

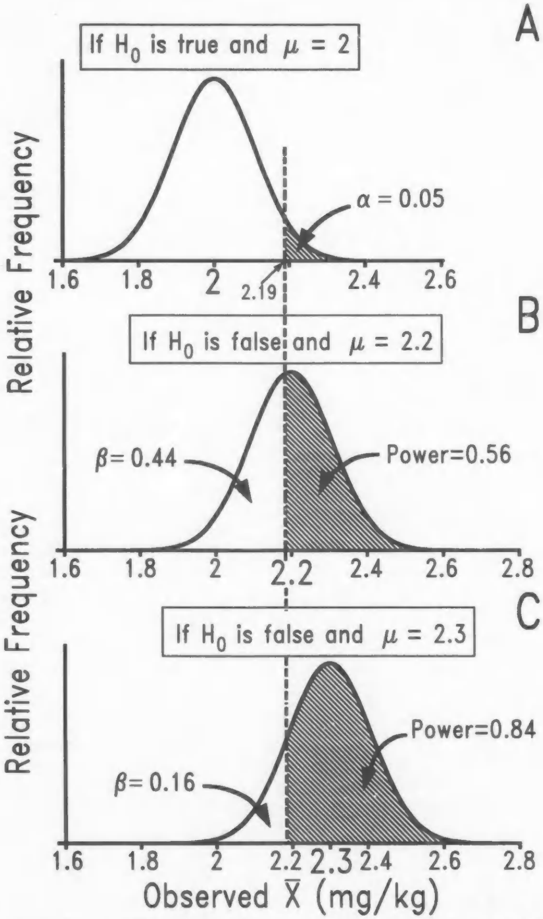

FIG. 3. Same as Fig. 1 except that parts B and C are for cases $\mu = 2.2$ and $\mu = 2.3$. Note that power increases (and β decreases) as the effect size increases, that is, as the true population mean gets further from $\mu = 2$. Again, in each distribution, a sample $\bar{X}$ to the right of the vertical dashed line would reject H_0, and to the left of it, would not reject H_0.

acceptably high probability) of finding a statistically significant result if the phenomenon exists (i.e. if H_0 is false).

For cases in which analytical formulae for power have not been derived, it is possible to use Monte Carlo simulation to generate power tables (e.g. Stephens 1974). This is done by assuming a true parameter value, repeatedly simulating a sampling scheme that includes random variability, performing statistical analysis of the data, and then quantifying the proportion of cases in which the H_0 was correctly rejected (e.g. de la Mare 1984; Peterman and Routledge 1983). Similar simulation procedures can be used to estimate required sample sizes and detectable effect sizes.

Note that by using power analysis, stronger inferences can be drawn, particularly in cases that fail to reject H_0, because information from power analysis differs from the normally reported *P* values and confidence intervals. For instance, the 95% confidence interval around a parameter estimate obviously reflects the data, but an estimate of the detectable effect size is influenced not only by the data but also by the desired power value (e.g. Rotenberry and Wiens 1985; Peterman 1989).

A Priori Power Analysis

A priori analysis is commonly used in fisheries before starting an experiment or management program to determine the sample size necessary to generate acceptably high power (high probability of correctly detecting an effect, if one exists) (e.g. McCaughran 1977; Green 1979, 1989; Fairbairn and Roff 1980; Vaughan and van Winkle 1982; Gerrodette 1987; Holt et al. 1987; Parkinson et al. 1988). It is also used to determine ahead of time how large an effect size would have to exist to give acceptable power, given the planned sample size (e.g. McCaughran 1977; Allen 1980; de la Mare 1984; Gerrodette 1987; Holt et al. 1987). Another use of a priori power analysis is to plan the magnitude of treatment perturbations (effect sizes) necessary to generate high power (e.g. Underwood 1981; Peterman and Routledge 1983). For example, one could determine the magnitude of changes in mesh size, allowable catch, or harvest rate required to generate a high probability that managers will be able to distinguish statistically the population's

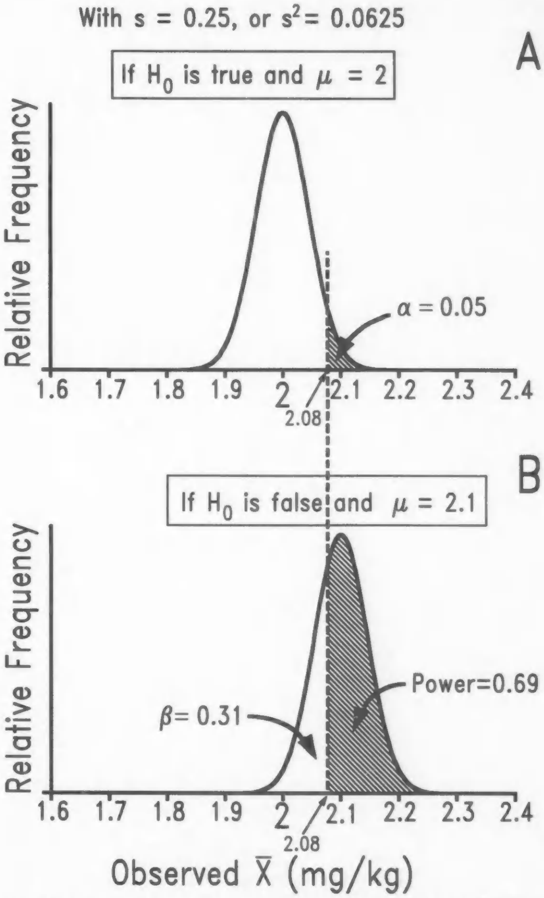

FIG. 4. Same as Fig. 1 except these sampling distributions have a smaller sample variance ($s^2 = 0.0625$ instead of 0.36) and hence the X-axis range is narrower (compare part B with Fig. 1B).

response to regulation changes from natural variability (e.g. Collie et al. 1990). Finally, a priori analysis can estimate power of proposed or currently operating experimental or management programs. If power is too low, remedial action can be taken by increasing the sample size or magnitude of the treatment effect, or by decreasing sampling variability (e.g. Fairbairn and Roff 1980; Peterman and Routledge 1983; de la Mare 1984; Gerrodette 1987; Holt et al. 1987; Peterman and Bradford 1987; Collie et al. 1990).

A Posteriori Power Analysis

In contrast to a priori analysis, a posteriori power analysis is relevant only in interpreting a statistical analysis of data that has already failed to reject the null hypothesis. The investigator would want to know whether there was no effect or whether the experiment simply had low probability of detecting an effect, even if one was present. There are disappointingly few recent published examples of a posteriori analyses in the aquatic sciences: some are cases in which the authors failed to find significant changes in abundance of invertebrates or fish as a result of predation (Johnson et al. 1987; Young and Gotelli 1988), experimental manipulation (Sweatman 1985), or current flow (Fegley 1987). Other papers more relevant to fisheries management questioned interpretations based on failures to reject H_0 when power was low: for example, the inadequacy of hatchery-produced sockeye salmon in British Columbia (*Oncorhynchus nerka*) (White 1988) and the lack of significant density-dependence in Oregon coho salmon (*O. kisutch*) (Peterman 1989). As an aside, note that if a statistical analysis already rejected the H_0 at the stated α, calculation of statistical power is not relevant (Cohen 1973).

Examples of Power Analysis

Details of selected examples illustrate the utility of power analysis in tests for existence of some biological phenomenon or relationship and tests for changes in abundance of a stock. I review several examples below to illustrate the variety of situations in which power analysis is informative.

Tests for a Biological Phenomenon or Relationship

British Columbia sockeye salmon provide an example of a posteriori analysis of fish hatcheries (White 1988). An 8-yr experiment comparing freshwater survival rates of wild and hatchery sockeye salmon in Cultus Lake failed to reject the H_0 of no difference (Foerster 1938). No information on power of these experiments was available, and decision makers concluded that there was indeed no difference. As a result they decided to close all sockeye salmon hatcheries in British Columbia in 1936 (Foerster 1968). Using Foerster's data and current methods to calculate power, White (1988) found that power was less than 0.34 due to small sample size and large variability, which meant that Foerster (1938) had at least a 66% chance of finding no difference, even if hatchery fish had survived better. Foerster's (1938) results were therefore too inconclusive to be used as evidence by decision makers. Depending on how successful sockeye hatcheries really were, British Columbia fisheries may have foregone additional revenue between the time they were closed and the introduction in the 1960s and 1970s of other large-scale enhancement techniques for sockeye salmon such as spawning channels and lake fertilization.

Nickelson (1986) tested the null hypothesis that marine survival rate of Oregon coho salmon (*Oncorhynchus kisutch*) was density-independent, i.e. unrelated to abundance of coho smolts going to sea. He was unable to reject the H_0 when he separately analyzed data for wild, private hatchery, and public hatchery stocks. Nickelson (1986) drew correct conclusions, but he did not report power values. However, an a posteriori power analysis of Nickelson's data under the assumption that his parameter estimates were true in nature found that power was less than 0.19 (Peterman 1989). In other words, even if marine survival were density-dependent in nature, there was at least an 81% chance of failing to detect it because of small sample sizes and large sampling variability. Unfortunately, some managers recommended building more hatcheries based on Nickelson's work (T. Nickelson, Oregon Dept. of Fish and Wildlife, Corvallis, OR, pers. comm.). In view of the low-power tests for density dependence, these recommendations were not justified.

Peterman (1989) also used the Oregon coho salmon data to solve for the effect size necessary to give a desired power level (i.e. the detectable effect size). This type of analysis is useful where it is not possible to postulate a narrow range of plausible values for effect size, but where it is possible to state effect sizes that are economically or biologically important (Underwood 1981; Rotenberry and Wiens 1985; Cohen 1988). In the case of the Oregon coho salmon, the true degree of density dependence (effect size) in marine survival rate would have to be very strong in order to achieve power above 0.8 ($\beta<0.2$) (Peterman 1989). Density dependence only slightly weaker than this strong detectable effect size could exist in nature and not be detectable, i.e. have an unacceptably low probability (<0.8) of showing up as significant in data analyses. This could produce an unacceptable economic payoff. Peterman (1989) discussed just such a case of an effect size that was not detectable but that was strong enough to lead to only 21% more adults when the number of juveniles was doubled. Calculation of detectable effect size thus informs managers that an economically important effect might exist, but that the experiment had an unacceptably small chance of detecting it.

The above types of a posteriori analysis could be usefully applied to any studies that failed to detect a significant relationship between variables such as (1) recruitment rate and various oceanographic measures, (2) abundance and predation rate, (3) growth rate and density, etc. One could estimate power for the given parameter estimates, determine how large an effect size could have been detected, and determine whether a biologically or economically important effect size could have been missed. These types of a posteriori analyses also apply to cases in which investigators fail to find a significant difference between groups of data and then pool them for further analysis.

A good example of a priori power analysis of a biological phenomenon is Arnason and Mills' (1987) paper. They explored via simulation the power of a test designed to detect handling mortality in fish mark–recapture experiments. They found that the test had low power (e.g. 0.45) even when the actual handling mortality rate (effect size) caused large overestimates (e.g. 117%) of abundance. Thus, even if there were sufficient handling mortality to create large biases in population estimates, users who applied this test would not often detect it. Hence, Arnason and Mills (1987) strongly recommend that users take all possible steps to reduce handling mortality.

Studies of isozyme variation that aim to identify separate populations of marine fishes assume that this variation follows some genetic model (Allendorf and Utter 1978). The chi-squared test is commonly used to test such models, but Fairbairn and Roff (1980) found via simulation that it has low power to detect deviations from hypothesized models, given the sample sizes that are normally used. This has led to erroneous conclusions about population structure (Fairbairn and Roff 1980), which may in turn have misled fisheries managers about the number of subpopulations they manage.

Tests for Changes in Abundance

Correct identification of changes in abundance of fish stocks is made difficult by large variability in mortality, growth, and reproduction rates, as well as errors inherent in stock assessment and sampling methods. Several statistical power analyses from impact assessment and resource management show that current methods of estimating populations have a low probability of detecting a significant change in abundance, should one occur.

Impact assessment

Postdevelopment monitoring of impacts is becoming more common in large-scale projects. Statistical power analysis is ideally suited to determine whether a proposed monitoring scheme is likely to detect the postulated effects, as illustrated by a study of the effect of electric power plants on white perch (*Morone americana*) in the Hudson River, New York (Vaughan and van Winkle 1982; Barnthouse et al. 1983). These authors used historical data on sampling variability of year-class strength to determine the time necessary to detect various degrees of decrease in white perch recruitment. With the most precise of their two sampling methods and with 10 additional years of monitoring data on recruitment, Vaughan and van Winkle (1982) found that recruitment would have to drop by 78% in order to provide a 75% chance of finding a statistically significant decline in abundance (point A on Fig. 5). If the management agency wanted to detect much smaller decreases in recruitment so that corrective action could be taken before fish abundance got too low, managers would have to settle for lower statistical power. To have a 50% chance (power = 0.5) of finding a 50% reduction in year-class strength, 19 yr of data would be required (point B on Fig. 5), or about half the expected lifetime of the power plants (Vaughan and van Winkle 1982). Current methods cannot attain power of 0.75 for that 50% reduction in recruitment, even with more than 100 yr of data. Results such as these show that statistical power analysis is essential to ensure that agencies realistically evaluate the capabilities of proposed postdevelopment monitoring schemes. Without such analyses, managers may implement inappropriate monitoring programs and not find statistically significant changes, even though large changes may have occurred. As this paper was going to press, I received a copy of the proof of Green (1989), which contains references to several impact assessments that included power analysis.

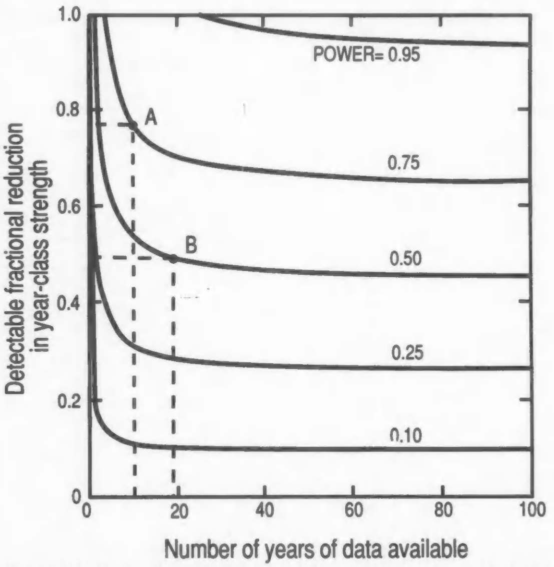

FIG. 5. Isopleths of power, or probability of detecting a statistically significant decline in recruitment of white perch in the Hudson River, New York. Power varies with sample size (number of years of data available) and effect size (minimum fractional reduction in recruitment that would be detectable at that power). These results are for $\alpha = 0.05$ and a coefficient of variation (CV) of 50% for the sampling method. See text for further explanation. Redrawn from Vaughan and van Winkle (1982).

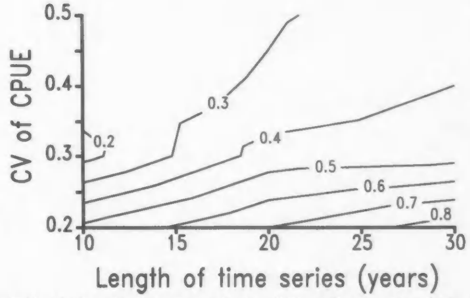

FIG. 6. Isopleths of power to detect a 50% reduction in whale abundance as a function of sample size (years of data) and sampling variability (coefficient variation in CPUE estimates). Data are from the weighted regression results in Table 4 of de la Mare (1984) in which CPUE was assumed to be nonlinearly related to whale abundance and $\alpha = 0.05$.

Resource management

De la Mare (1984) examined the power of the International Whaling Commission's (IWC) data on catch per unit effort (CPUE) to detect changes in whale stock abundance. His study was prompted by the IWC's 1983 "New Management Procedure," which stated that as long as the slope of a linear regression on at least 10 yr of CPUE values for a stock was not significantly different from zero, that stock would be classified as a provisional or sustained management stock, implying that existing harvest rates would be maintained (de la Mare 1984). However, de la Mare (1984) recognized that variability in CPUE estimates could easily mask true trends in stock abundance and thereby mislead the IWC. Using Monte Carlo simulations to explore how a wide range of assumptions affected β, he found that under most conditions, IWC scientists would have a high probability of not rejecting the H_0 of constant whale abundance, even when the stock had decreased dramatically; i.e. power is generally low (Fig. 6). For instance, in the case with a 50% true decrease in abundance (effect size) over 20 yr, power would be 29 to 70%, depending on the coefficient of variation (CV) in CPUE estimates. Thus, de la Mare showed that the IWC's New Management Procedure had a high risk of leading to an incorrect and perhaps costly conclusion. The Scientific Committee of the IWC was aware of de la Mare's work but no action was taken because of the imminent moratorium on commercial harvesting of whales that was to begin in 1986 (Douglas Chapman, University of Washington, Seattle, WA, pers. comm.).

In a study of two common stock assessment methods (trawl survey of prerecruits and virtual population analysis, VPA), Peterman and Bradford (1987) used an empirically based simulation model of a flatfish, English sole (*Parophrys vetulus*), off the west coast of North America to estimate the probability that a desired trend in abundance could be generated and then have a high probability of being correctly detected by managers. The reason for combining the generation of a true trend with its probability of detection was that managers not only want to take regulatory actions that will cause a certain change in abundance of a stock (e.g. to increase its productivity), but they also want to have a high probability of observing a significant response to those actions. Without the latter, they might unnecessarily restrict fishing, for example, with obvious costs to fishermen. Under most realistic conditions, the probability of both causing and correctly detecting desired population trends in English sole was usually less than 0.6 (Peterman and Bradford 1987). An approximately four-fold increase in sampling effort for the trawl survey would only increase power by 5–10%.

Gerrodette (1987) explored power to detect trends in marine mammal populations. He derived general relationships among power and various attributes of population estimation such as number of census flights per year and duration of the data set. He then applied his analysis to California sea otter (*Enhydra lutris*), which prey on commercially important species such as lobster, crab, and abalone. California fishermen and managers wish to know whether otters or other marine mammals are increasing in abundance because of potential competition with fishermen for prey. Gerrodette (1987) found that with a 5% annual rate of increase in otters, it would take at least 7 yr to detect an increase with acceptably high power. At that point the population would actually have increased by 41%, an undesirably large amount if remedial action to decrease abundance were required.

Holt et al. (1987) used Gerrodette's (1987) equations to design a program for monitoring populations of dolphins, which are harvested incidentally by purse seiners in the eastern tropical Pacific tuna fishery. They found that current survey methods would have high power only if there were relatively large rates of decrease (effect sizes) in dolphin populations. For example, with two research vessels operating over 5 yr, power would be ≥ 0.8 only if the dolphins decreased by 10% per year (41% over the 5 yr), at $\alpha = 0.05$. Power of these 5-yr programs increased with increased effect size (percent decline in abundance per year) and with increased α (Fig. 7A). If scientists want equal probability of making type I and type II errors ($\alpha = \beta$), then the *total* reduction in dolphin abundance that must occur to achieve the associated desired power decreases as α and β increase, for a given *annual* rate of decline in abundance (Fig. 7B).

Fish and marine mammals are of course not managed solely on the basis of estimated trends in abundance. When setting fishing regulations, managers also consider other information such as current stock abundance, age structure, oceanographic conditions, etc. However, trends in stock abundance are very important because they heavily influence conclusions drawn about the success or failure of past management actions. Incorrect conclusions about past successes will therefore mislead managers about the utility of certain actions in achieving objectives in the future.

Implications of Ignoring Power

It should be clear from the examples above not only that knowledge of power can be beneficial, but that ignorance of it can have serious consequences. Impact assessments and post-development monitoring programs that have low power are inadequate and will not meet their objectives (e.g. McCaughran 1977; Vaughan and van Winkle 1982; Green 1979, 1984; Millard 1987). They could mislead agencies because they would have little chance of finding statistically significant effects, even if true effects were large. Workers who ignored power might proceed under the delusion that if statistically significant effects existed, they would be detected. Thus, low-power impact assessment experiments could generate type II errors and high costs of depletion of aquatic resources. Hayes (1987) reviewed the toxicology literature (where we might expect to find high power), and if his results are indicative, we are not likely to find encouraging results in the impact assessment literature.

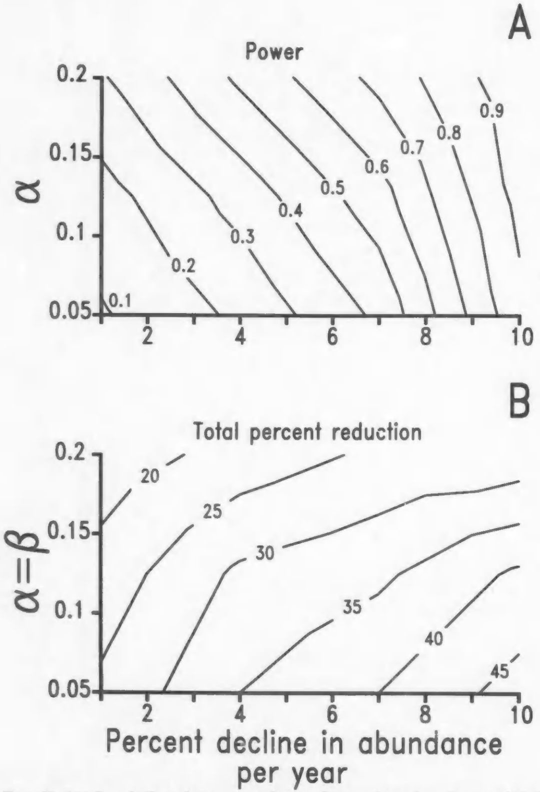

FIG. 7. (A) Isopleths of power to detect decreasing abundance of dolphins as a function of the effect size (percent decline in abundance per year) and α, given a 5-yr survey with CV = 0.14 (data from Table 7 of Holt et al. 1987). (B) Isopleths of the total percent reduction in dolphin abundance from its initial level that would occur by the time that the probability of seeing a significant decline reached 1 − β (data from Table 8 of Holt et al. 1987). The total percent reduction is shown as a function of effect size (percent decline in abundance per year) and α, which is set equal to β. These again are results for CV = 0.14. Note in part B that desired power was set by assuming that one wanted to be as conservative about making type II as type I errors, i.e. α = β.

Hayes found high power in only 19 out of 668 reports that failed to reject the H_0.

In the case of research that attempts to test for biological relationships or effects of various treatments, not knowing power before an experiment is begun can lead to implementing experiments that have little chance of detecting an effect, even if one exists (Green 1979; Millard 1987). Scientists may thereby miss opportunities to increase understanding of the mechanisms of population change and improve fisheries management. If a posteriori power analysis shows that a given experiment on a biological relationship had lower power, the experiment might have to be repeated, at considerable cost. Such costs can be minimized by designing a high-power experiment initially.

Although I do not want to imply that the H_0 will always turn out to be false when we initially fail to reject it, the general conclusion from the examples in the previous section, "Tests for Changes in Abundance," is that many of our stock assessment methods have low power, or poor ability to detect changes in true population abundance. Managers that do not know that power is low may take actions that either risk overharvesting or underutilizing the stock. It is unsettling to realize that many fisheries are still managed by principles similar to those in the IWC's 1983 New Management Procedure. As a consequence, until there is evidence for a significant decline in a stock, management agencies have difficulty justifying reduction in fishing effort (Saetersdal 1980) because they are under considerable pressure from fishing industry. As well, scientists generally want to be reasonably certain that changes in fish stocks are occurring before making strong recommendations to managers. In other words, scientists want to be able to reject the null hypothesis of no change in abundance before recommending some change in management regulations. However, by focussing on rejections of H_0, scientists usually forget about type II error. Saetersdal's (1980) paper shows that scientists' focus on rejections of H_0 contributed to the collapse of several North Atlantic and North Sea pelagic fish stocks because large decreases in abundance occurred before strong actions were recommended by scientists to control fishing. I would add that ignorance of the probability of a type II error likely contributed to the collapses as well. Had β or detectable effect size been reported, managers might have acted more appropriately.

The long-standing controversy over the effect of spawning stock biomass on recruitment (Rothschild 1986) is another topic in which failure to examine the probability of making a type II error may have contributed to the collapse of stocks. Variability in spawning stock usually does not explain much of the variability in recruitment (Rothschild 1986). Such poor fits led some scientists and managers to conclude that spawning stock biomass has little effect on recruitment over a wide range of stock abundances. This is turn led some management agencies to use Beverton-Holt (1957) type yield/recruit models, which did not have an explicit relationship between spawning stock and recruitment and which implicitly assumed "that recruitment does not decline under the pressure of fishing" (Cushing 1974). When stocks collapsed due to poor recruitment, questions were raised about the assumption of no relationship between spawners and recruits (Cushing 1974). If the probability of making a type II error when fitting stock–recruitment relationships had been routinely reported by scientists along with detectable effect sizes, the values would likely have been high due to the large variability inherent in such data and the relatively short time series normally available. Thus, there might have been earlier development of more appropriate techniques, such as dynamic pool models (Pitcher and Hart 1982), that take into account possible stock–recruitment relationships and thereby help managers avoid overharvesting.

Costs of Errors

The cost of type II errors often exceeds the cost of type I errors. For example, if a stock is rapidly declining in abundance but is being managed as if it were relatively constant because of low-power data, type II error could lead to collapse of the stock and loss of all future revenue. Type I error, on the other hand, would arise if data incorrectly led to the conclusion that the stock was declining and harvesting was reduced. The cost of reduction in fishing in the latter case would be smaller than that caused by the total closure of the fishery unless discount rates and present value concepts (Clark 1976) altered their relative values.

Most scientists and decision makers do not realize that taking action as a result of a statistical analysis that fails to reject an

H_0 automatically implies an assumption about the relative costs of type I and type II errors, quite independent of their real costs (Toft and Shea 1983; Cohen 1988). In particular, where β is $\geqslant\alpha$, they assume implicitly that the costs of type I errors exceed those of type II errors if they act as if H_0 were true (Toft and Shea 1983). For example, suppose that data from an experiment on the effect of a pollutant on fish did not reject the H_0 of no effect at $\alpha=0.05$ and that the best estimate of the effect size from current data gave a $\beta=0.4$. Suppose that decision makers wanted to take the action with the lowest expected cost of an error (expected cost = probability of occurrence × cost if it occurs). If data analysis failed to reject H_0 and if they took action to avoid making a type I error (assuming the H_0 to be true and permitting the industry to discharge the pollutant), then they would implicitly be assuming that the expected cost of a type II error is less than the expected cost of a type I error. This is demonstrated by solving for the ratio of costs of type II to type I errors, C_{II}/C_I, given α and β and assuming that action was taken as if H_0 were true: $\alpha C_I > \beta C_{II}$, or $\alpha/\beta > C_{II}/C_I$. Since $\alpha=0.05$ and $\beta=0.4$ here, $0.125>C_{II}/C_I$, or $C_I>8C_{II}$. In other words, by taking the action that they did, the managers implicitly assumed that the cost of making a type I error was more than eight times the cost of a type II error. But as noted above, type II errors are often more costly than type I errors in fisheries management. Such implied cost ratios are rarely reported. If they were, managers might take actual costs of the two types of error into account explicitly and perhaps make different decisions.

On a related point, suppose that managers want to be as conservative about making type II as type I errors, and they define this to mean that they want to have equal expected costs for type I and type II errors. In the simplest case, if the cost of a type I error equals the cost of a type II error, then the level of β below which an experiment is acceptable would be equal to α. Setting the α then would determine β. If however, a type II error is twice as costly as a type I error, then managers should set $\beta=\alpha/2$ (Cohen 1988). This means that to justify acting as if H_0 were true after a statistical analysis failed to reject the H_0, the a posteriori β would have to be $\leqslant\alpha/2$. This is only one possible method of taking relative costs and probabilities into account; more complex approaches are widely available in the decision analysis literature (Raiffa 1968; Berger 1985).

Responses by management agencies to rectify situations where a type II error was made could incur the costs of both type I and type II errors. For example, suppose a study showed no significant effect of pulp mill effluent on fish and led managers to decide to take no action against a pulp mill. If at some later date, new data showed a significant effect (i.e. that a type II error had been made earlier), then managers would impose pollution control regulations on the pulp mill. Those regulation costs would include the costs if a type I error had been made in the earlier situation (costs of installing pollution controls), plus the costs of the type II error, already suffered (perhaps lower fish yields, human health costs, etc.) (Fig. 8). So in this type of situation, the total cost of the decision path that reflects acting as if the H_0 were true will likely be larger than the path that assumes the H_0 to be false (compare Figs. 8 and 9).

A final point about the pulp mill example is that costs of type I errors can be incurred by different groups than costs of type II errors. Managers can take this into account through their normal decision making procedures and priorities.

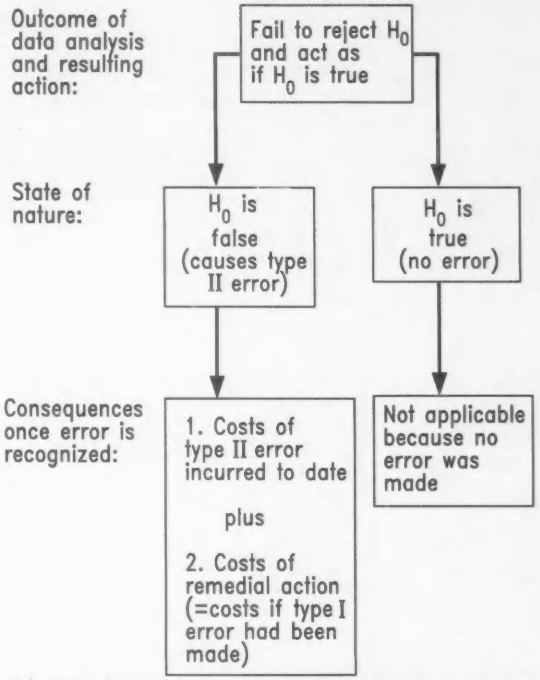
Outcome of data analysis and resulting action:
Fail to reject H_0 and act as if H_0 is true
State of nature:
H_0 is false (causes type II error)
H_0 is true (no error)
Consequences once error is recognized:
1. Costs of type II error incurred to date
plus
2. Costs of remedial action (=costs if type I error had been made)
Not applicable because no error was made

FIG. 8. Hypothetical sequence of events following the failure to reject H_0. The type of error, if any, depends on the true state of nature, and if an error is made, there are consequences once the error is recognized at some later date.

Recommendations for Scientists

These observations on statistical power and related concepts lead to a series of recommendations for both scientists and decision makers. It is important to recognize their separate roles. Fisheries and aquatic scientists often deal with uncertainty because their systems are highly variable and contain multiple causal mechanisms. In effect, these scientists are responsible for assessing and reducing uncertainty by formulating and testing hypotheses. They therefore must convey all aspects of their uncertainty to decision makers, who decide which uncertainties to weight more heavily.

To assess and reduce uncertainty effectively, scientists should follow several steps, some of which are already standard practice and others of which are not. The following steps should be adapted to circumstances, depending on whether scientists are doing impact assessment or are involved in research on natural or man-manipulated systems.

The first six recommendations below are relevant to a priori power analyses, as defined earlier.

(1) Fisheries and aquatic scientists need to design experiments or impact assessments to have high power (Green 1979; Bernstein and Zalinski 1983; Andrew and Mapstone 1987; Millard 1987; Parkinson et al. 1988). This goal should be combined with other aspects of rigorous experimental design (Bernstein and Zalinski 1983; Green 1984; Hurlbert 1984; Millard and Lettenmaier 1986; Stewart-Oaten et al. 1986; Walters et al. 1988) to increase the chances of distinguishing clearly among alternative explanations of the data. Obviously, this goal

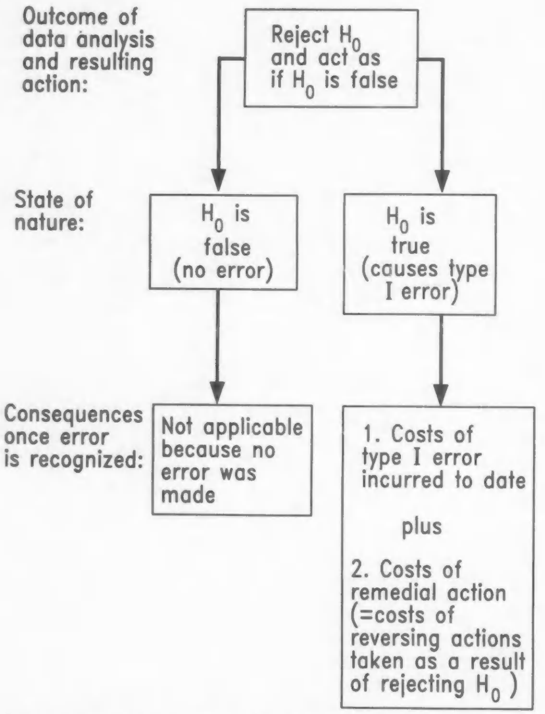
Outcome of data analysis and resulting action:
Reject H0 and act as if H0 is false
State of nature:
H0 is false (no error)
H0 is true (causes type I error)
Consequences once error is recognized:
Not applicable because no error was made
1. Costs of type I error incurred to date
plus
2. Costs of remedial action (=costs of reversing actions taken as a result of rejecting H0)

FIG. 9. Hypothetical sequence of events following the rejection of H_0 (cf. Fig. 8).

requires careful formulation of testable null and alternative hypotheses (Green 1979). Experimental design principles should also be used to devise changes in management regulations to help avoid confounding the effects of management manipulations with effects of natural changes (Bernstein and Zalinski 1983; Walters 1986; Walters et al. 1988).

(2) A priori analyses should explore the effect on power of several plausible assumed effect sizes, different durations of experiments or other sample size-related variables, and various levels of measurement error (e.g. Peterman and Routledge 1983; de la Mare 1984; Gerrodette 1987; Parkinson et al. 1988). In cases where there are complex responses, Monte Carlo simulations should be done to estimate the probability of correctly rejecting an H_0, if some assumed effect size is present.

(3) A slight variation on the above is to assume a desired α, β, sample size, and sample variance, and then solve for the effect size that could be detectable with such an experiment (Rotenberry and Wiens 1985; Cohen 1988; Peterman 1989). If this detectable effect size is large relative to that which is plausible in nature or that which is economically or biologically important, then a larger sample size or a more precise sampling scheme will be necessary.

(4) Scientists should consult easy-to-follow papers on statistical power analysis (e.g. Toft and Shea 1983; Rotenberry and Wiens 1985; Andrew and Mapstone 1987) and texts (Dixon and Massey 1969; Winer 1971; Kramer and Thiemann 1987; Cohen 1988). As well, Cohen (1988) cites several microcomputer programs that can assist with power analysis (Anderson 1981; Haase 1986; Dallal 1987; Borenstein and Cohen 1988). O'Brien (1982) also discusses ways to do power analysis with any ANOVA or regression software.

(5) Scientists should estimate the power of stock assessment methods to detect changes in abundance and explore via simulation how plausible types of imprecision and inaccuracies can affect power (e.g. de la Mare 1984; Peterman and Bradford 1987; Lapointe et al. 1989). Scientists should continue to develop more precise methods of estimation because imprecise measurements decrease power.

(6) By departing from the *arbitrary* tradition of setting $\alpha = 0.05$, and instead increasing α to 0.1 or some other value, fisheries and aquatic scientists can obtain higher power (Fig. 2). Increasing α is particularly relevant to cases where the cost of type II errors is much larger than the cost of type I errors.

The next six recommendations are relevant to a posteriori power analyses, in which an H_0 was not rejected.

(7) If a completed statistical analysis fails to reject the H_0, β or power should be calculated and reported for several plausible effect sizes, including the point estimate of the effect size obtained in the original statistical analysis. Results of such power analyses should be presented to decision makers, preferably in a readily understood, graphical form.

(8) The Rotenberry and Wiens (1985) method mentioned in recommendation (3) above should also be applied in an a posteriori analysis to determine the effect size that was detectable by the experiment (e.g. Vaughan and Van Winkle 1982; de la Mare 1984; Peterman 1989).

(9) Scientists should explicitly report the *biological* ramifications of type II errors. Economists can then provide managers with estimates of the relative *economic* costs of these errors.

(10) It would be useful to review past impact assessments, following the search method that I report here for fisheries journals, to determine how frequently power was ignored and what detectable effect size existed. The more statistical power analyses of impact assessments there are that show low power, the more likely it is that we will change the current practice of doing short-term and perhaps low-power assessments.

(11) Scientists *must not* assert, either explicitly or implicitly, that "no effect" exists when a data analysis fails to reject some H_0. They must also not draw conclusions or make recommendations based on the failure to reject H_0 unless there is high power. Yet as shown by the literature review in Table 2, many fisheries scientists make interpretations or recommendations based on failing to reject the H_0, without even considering the possibility that their analyses had low power. This practice *must* change if scientists are to improve the quality of interpretations of their results.

(12) Finally, fisheries and aquatic scientists should apply statistical power concepts to all areas of research and management. We should always consider power and detectable effect size when planning research programs, and should ask about these quantities whenever we see results that fail to reject some H_0. This should be the practice regardless of the topic — impact assessment, comparison of outcomes from different management regulations, tests for density-dependent catchability coefficients, importance of the foreign drift net fishery in the North Pacific, toxicology, tests for effects of oceanographic variables on fish recruitment, etc.

Recommendations for Decision Makers

For simplicity, I use the term "managers" below to mean anyone involved in decision or policy making and management of aquatic resources.

(1) Managers should familiarize themselves with the above recommendations for scientists to know what to expect from them.

(2) In particular, managers should require scientists to report β along with the standard P values associated with making type I errors to enable managers to make appropriate risk tradeoffs.

(3) Managers should not jump to the conclusion that there is no effect of some factor (such as effect of a dam on mortality rate of migrating juvenile salmon) when scientists report that a data analysis failed to reject the null hypothesis of no effect. There could indeed be no effect, but there could also be a large effect which is simply masked by a low-power experiment. Actions should be taken that are based on the H_0 of no effect being true only if power is acceptably high and if the ratio of expected costs of type I and type II errors meets managers' requirements. If power is not acceptably high, the experiment is inconclusive. When documenting the reasons for their decisions, managers should mention power, other uncertainties, and expected costs of type I and type II errors.

(4) When planning budgets, managers should either give scientists sufficient funds and time to carry out a high-power test of the H_0, or not fund them at all. Low-power tests are worse than no tests because, (a) they may create the illusion that something useful has been learned concerning the hypothesis, and (b) they may have to be repeated with added cost. Sufficient time and funds are major issues that are not easily resolved. However, unless terms of reference for impact assessments are changed to permit sufficient time to do high-power tests of null hypotheses, low-power assessments may mislead decision makers (Bernstein and Zalinski 1983; Millard 1987).

(5) As noted in the first recommendation for scientists above, managers should work with scientists to design management actions or changes that will permit future evaluation of how well regulations have worked. The effect size and sample size of those treatments should be large enough to have high probability of correctly detecting the response of the population.

(6) Most power analyses that have been done in fisheries management show that population changes can be masked by low-power stock assessment methods (as shown above for whales, dolphins, English sole, and white perch). In other words, those methods can often fail to reject the null hypothesis of no change in abundance, even when large changes have occurred. This observation, combined with the evidence that overfishing has caused numerous fish stocks to collapse (e.g. Paulik 1971; Regier and Hartman 1973; Cushing 1974; Parrish and MacCall 1978; Saville 1980; Thompson 1981; Selgeby 1982; Clark et al. 1982; Beverton 1983; Butterworth 1983; Allen and Kirkwood 1988), strongly suggests that managers should be more cautious. They should manage conservatively from the standpoint of the stock when statistical analyses fail to show a time trend in abundance or an effect of some variable, and when power is low or unknown. Our low-power stock assessment methods may take a long time to correctly identify the effect of fishing on a stock, during which time the fishing fleet and associated industries normally develop rapidly (Paulik 1971; Pearse 1979; Beverton 1983). Thus, a practical and cost-effective conservative strategy would be to impose severe limitations on development of total fishing power early in a fleet's development, rather than waiting until a biological or overcapitalization crisis appears (e.g. Meany 1979; Francis 1986).

(7) For the foreseeable future, we will probably be faced with numerous situations where, (a) data analyses fail to reject some H_0 of no effect, (b) power is low, and (c) some decision needs to be made. This suggests a more conservative approach, which would require decision makers to reverse the burden of proof, as explained below (Carswell and Swaigen 1978; Belsky 1984).

Reversing the Burden of Proof

Presently, the onus is on most management agencies to show that fishing under current conditions is having a detrimental effect on fish stocks (i.e. reject the H_0 of no effect) before regulation changes can be imposed and accepted by the fishing industry (e.g. Caddy and Gulland 1983). An alternative is to put the burden of proof on the industry to show with high power that fishing does *not* have a detrimental effect (i.e. fail to reject H_0 but with high power) (Wright 1981; Peterman and Bradford 1987). This major reversal from current practices is particularly justified in cases in which, (a) the cost of type II errors is likely to be much larger than the cost of type I errors, as would be true in many toxicology and health questions, and (b) there is a history of similar situations in which the H_0 of no effect or no change in abundance was eventually rejected, after early data did not reject H_0, as was the case with many collapsed pelagic fish stocks (Saetersdal 1980).

It may be in the long-term interests of the fishing industry to follow this new approach to the burden of proof because it will lead to more conservative management, from the standpoint of stock viability. The frequency of collapsed stocks should decrease and the revenue from harvests should become more sustained.

Precedents for reversing the burden of proof already exist in procedures for putting new pesticide, food, or drug products on the market (Belsky 1984; Schrecker 1984), possibly because of the high health costs associated with a type II error. Why should we manage our fishery resources any differently?

Scientists and managers should seriously consider reforming the burden of proof because the evidence reviewed above shows we are commonly in low-power situations, where detectable effect sizes are larger than is desirable and the costs of failing to detect effects are high. Changes could be made in legislation to prevent any discharge of potentially hazardous materials (for example) until industry showed that the H_0 of no effect was not rejected and that power was high. However, a reversal of burden of proof is a major shift from current practice, and while such changes have been made in some cases (Belsky 1984; Schrecker 1984), legislated changes usually occur slowly. In the interim, managers could modify management standards in at least three ways to partially achieve the same end (Schrecker 1984). (1) Based on past management experience, analysts could set H_0 to be some effect size *other than* no effect. Discharging of a pollutant or increased fishing could only be permitted if that H_0 were rejected in the permissible direction (e.g. towards absence of a harmful effect). I am currently developing a method to set this value of H_0 objectively; the method will modify an existing null hypothesis of no effect by the detectable effect size. (2) Managers and scientists could increase the acceptable α to increase the chances of rejecting a null hypothesis of no effect. This may take time to gain acceptance but it could be done without legislative changes. (3) Managers could set acceptable power high enough to realistically reflect the relative costs of type I and type II errors, as noted earlier. They would have to agree to take actions that could lead to a type II error (i.e. acting as if H_0 were true) *only* if power were greater than that acceptable level. This approach appears best because it can be implemented immediately without going through legislative channels and does not entail changes to the deeply entrenched $\alpha = 0.05$.

Concluding Remarks

Statistical power concepts provide a quantitative framework for analysis that is particularly appropriate for research on aquatic ecosystems. Such systems are, by their nature, highly variable and difficult to measure with precision and accuracy. Quantification of the probability of making both type I and type II errors can help to improve the design of research and management experiments and improve the inferences and recommendations that result from them.

The tradition of ignoring power is not restricted to the aquatic sciences or even ecology in general (e.g. Brewer 1972; Cohen 1973; Hayes 1987). Cohen's (1962) retrospective analysis even showed that some ideas in psychology were erroneously established because of low-power tests. A similar retrospective analysis of published work in fisheries and aquatic sciences would be a useful and revealing exercise. The aim would be to identify long-standing ideas that have persisted (unjustifiably) because tests that failed to reject some H_0 had low power.

It is not clear why β, power, and detectable effect size have traditionally been ignored in favor of reporting the probability of making a type I error. It is conceivable that most researchers simply have not been exposed sufficiently to the idea of type II errors. Most introductory statistics texts mention the topic only briefly, and very few texts go further to show how to calculate power, detectable effect size, and required sample size for the common statistical methods (e.g. Dixon and Massey 1969; Winer 1971; Cohen 1988). Furthermore, computer packages for power analysis have only recently become available (see recommendation (4) for scientists). Another possibility may be that most researchers have not recognized the potentially high cost of making type II errors. Most researchers also may not understand how knowledge of power, detectable effect size, or other related quantities can improve their work. The lack of examples in the literature may contribute to this lack of awareness, hence this review. Whatever the explanation, scientists must now depart from tradition and begin to apply routinely the concepts related to statistical power.

Fisheries scientists frequently deal with situations in which there can be large costs of mistakenly assuming there is no effect (of fishing, of some chemical, etc.). It is therefore imperative that we treat what little data we have as completely and as rigorously as possible by utilizing information on β, power, and detectable effect size. Of course, this will not guarantee success, but it will increase our chances of making better decisions when managing our natural resources.

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Leaky Filters: A Warning to Aquatic Ecologists

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Stockner, J. G., M. E. Klut, and W. P. Cochlan. 1990. Leaky filters: a warning to aquatic ecologists. Can. J. Fish. Aquat. Sci. 47: 16–23.

We examined the retention characteristics of commonly used 0.2-μm nucleation-track (Nuclepore®, Poretics®), polymer (Millipore®, Sartorius®) and inorganic membrane (Anopore®) filters. Scanning electron micrographs of the filter surface showed many to contain large holes or pores, some 5× larger than the manufacturer's stated nominal pore diameter. Electron micrographs of filtrates from both fresh and seawater samples contained a variety of organisms, including viruses, ultramicrobacteria, bacteria, phototrophic picoplankton, and larger nano- and microphytoplankton (e.g. diatoms), which we believe passed through the large openings. Total particles in the size range 1.0–12.8 μm passing through the various 0.2-μm filters tested ranged from 2.2 to 14.3%, with 'best' retention (>97%) by the Anopore®. Average particle retention for all 0.2-μm filters tested was 92.5%. Higher passage rates (lower retention) are predicted for even smaller (<1.0 μm) particles (prochlorophytes, bacteria, viruses) and investigators are urged to use care when using polycarbonate or matrix type filters for partitioning size fractions for chemical, physiological, and ecological work, and caution when interpreting results, especially if separations have not been verified by microscopy, incubation, or culture.

Les auteurs ont étudié les caractéristiques de rétention de divers filtes de 0,2-μm couramment utilisés, à savoir : les filtres obtenus par nucléation (Nuclepore®, Poretics®), les filtres de polymères (Millipore®, Sartorius®) et les membranes inorganiques (Anopore®). Des micrographies, au microscope électronique de balayage, de la surface des filtres ont montré que bon nombre de ces filtres présentaient des trous ou des pores importants dont le diamètre pouvait être de 5 fois supérieur au diamètre nominal des pores indiqué par le fabricant. Les micrographies électroniques de filtrats d'échantillons d'eau douce ou de mer ont montré la présence de divers organismes, dont des virus, des ultramicrobactéries, des bactéries ainsi que des organismes du picoplancton phototrophe et du nano et du microphytolancton plus gros (p. ex. : des diatomées), que les auteurs estiment être passés par les gros pores. Le pourcentage total des particules de la gamme de tailles, 1,0 – 12,8-μm qui ont réussi à traverser les filtres de 0,2-μm testés variait de 2,2 à 14,3 %, la « meilleure » rétention (97 %) a été obtenue avec les Anopore.® Le taux de rétention des particules moyen de l'ensemble des filtres de 0,2-μm testés s'est élevé à 92,5 %. Les auteurs prévoient des taux de passage supérieurs (plus faible rétention) pour les particules plus petites (prochlorophytes, bactéries, virus) et soulignent la nécessité pour les chercheurs de faire preuve d'attention au cours de l'utilisation de filtres de polycarbonate ou de type matriciel pour le fractionnement en gammes de tailles au cours de travaux chimiques, physiologiques ou écologiques et au moment de l'interprétation des résultats, surtout lorsque les fractions obtenues ne sont pas vérifiées par microscopie, incubation ou culture.

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In the last two decades limnologists and oceanographers have become more aware of the significance of protists in nutrient recycling and carbon metabolism in pelagic ecosystems (Johannes 1965; Pomeroy 1974; Azam and Hodson 1977; Williams 1981). With this resurgence of interest in microbial ecology came the requirement for size-fractionation of samples. Early workers looked only at coarse separations (< or >10 μm) that were easily accomplished by fine-mesh screens (e.g. Nitex®) or very coarse fiber filters (Holmes and Anderson 1963; Gliwicz 1967; Malone 1971; Gelin 1975). However, in the last decade more stringent protocols now necessitate finer particle size partitioning (Sieburth et al. 1978; Fuhrman and Azam 1982; Johnson and Sieburth 1982; Li 1986; Waterbury et al. 1986). Some of the early glass fiber and polymer filters retained most particles with diameters between 0.4–0.7 μm (Harvey 1950; Oppenheimer 1952), but neither acted as sieves to permit more precise size separations to be made. This requirement was largely met by the nucleation-track polycarbonate filter that acted as a true sieve (Sheldon 1972; Brock 1983). Several critiques of their effectiveness at particle retention have been written (Sheldon 1972; Salonen 1974; Hobbie et al. 1977; Craig 1986; Li 1986), but none have provided electron micrographs of filtrates from 0.2-μm pore diameter filters to document the nature of the passed particles.

Polycarbonate and polymer membrane filters of 0.2-μm nominal pore diameter are among the most widely used today by aquatic ecologists interested in measuring production and biomass and in determining the chemical composition and concentration of particulate and dissolved material. Using scanning and transmission electron microscopy (SEM, TEM) we have focused our investigation on the size and composition of particles passing three types of filters: (1) nucleation-track polycarbonate (Nuclepore®, Poretics®, etc.), (2) organic polymer (Sartorius®, Millipore®, etc.) and (3) inorganic membrane (Anopore®). The purpose of this communication is to alert investigators of the possibility of incomplete retention of bacteria, phototrophic picoplankton, and nanoplankton by these filters, and to discuss some of the implications of this 'leakage' on results of pertinent physiological and ecological studies.

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Methods

Filters were obtained from plankton ecology laboratories at the University of British Columbia, departments of Oceanography and Botany and at the West Vancouver Laboratory, Department of Fisheries and Oceans. Filters were purposely taken from existing stocks that were in daily use in field and laboratory studies. For SEM and TEM work our fresh water samples were taken in July and September, 1988 from Sproat Lake (49°14′N, 125°06′W), an ultraoligotrophic, warm-monomictic lake on Vancouver Island, British Columbia (Stockner and Shortreed 1985). Seawater samples taken in November, 1988 came from the Strait of Georgia, Burrard Inlet, adjacent to the West Vancouver Laboratory (49°20′N, 123°14′W). Water samples were taken at a depth of 0.5 m and were kept cool until processed, usually within 24 h of collection. Test filters were placed in acid-cleaned and double-distilled water rinsed Millipore® or Gelman® filtration units and between 20–300 mL of sample was filtered at a vacuum pressure differential of between 50–90 mm Hg (680–1225 Pa). Filtrates were concentrated by two or three repeat filtration passes onto either 0.1 or 0.2-μm Nuclepore® filters.

For SEM, filtrate samples retained after repeat passes on an 0.2-μm Nuclepore® filter were fixed for 1 h in 1.5% osmium tetroxide (OsO_4) using phosphate buffer at pH 7.5. After dehydration in a graded ethanol series, specimens were critical-point dried, gold-coated and viewed with a Cambridge Stereoscan® 250T scanning electron microscope. In addition, test filters were randomly chosen from the laboratory stock, gold-coated, and SEM examined for possible defects. For TEM, filtered cell samples from 0.2-μm Sartorius® filtrate were fixed for 2 h in 2% glutaraldehyde (using the same buffer as in SEM, above), postfixed for 1 h in 1% osmium tetroxide, dehydrated with ethanol and then embedded in Epon 812. Ultra-thin sections were viewed with a Zeiss EM 10A electron microscope.

To estimate numbers of particles passing filters we obtained seawater samples in September, 1989 from the Strait of Georgia, Burrard Inlet, adjacent to the West Vancouver Laboratory from a depth of 1 m. Samples were kept cool and in the dark until processed, within 2–4 h of collection. The concentration and distribution of particles in the filtrates of five different 0.2-μm filter types (see Table 1) were determined with a Coulter Counter® (Model TA II) equipped with the population accessory (enabling particles to be counted into multiple channels based on their volume) and a 30-μm aperture. The Coulter Counter® was calibrated with 2.02-μm latex microspheres. The filtrate from three separate filters of each type were examined with the particle counter on 11 channels covering a range of particle size diameter from 1–12.8 μm. The lower three channels, covering the 0.6–1.0 μm size range were not utilized enabling us to avoid diluting the sample, keep coincidence negligible (<5%) and decrease the risk of including spurious counts from electronic interference (noise) (Sheldon 1978; Parsons et al. 1984). Each filtration apparatus consisted of a Millipore® borosilicate glass funnel and base equipped with a removable stainless steel filter support screen atop a teflon gasket. The filtrate (10–15 mL) was collected directly into a clean, dry 30-mL polypropylene bottle after an initial rinse of the system (including filter) with filtrate (5 mL). In order to eliminate risk of damaging filters they were only handled by their edge with smooth-tipped filter forceps. We attempted to minimize contamination of filtrate by scrupulously cleaning all filtration apparatus and collection bottles with 10% HCl (v/v), repeatedly rinsing with distilled, deionized water, and autoclaving prior to use. To minimize cell rupture (e.g. see Goldman and Dennett 1985), all filtrations were conducted at low vacuum pressure — <80 mm Hg (1090 Pa), and were terminated prior to the filter becoming dry. Filtrations were conducted in a laminar-flow hood. The counts in the raw seawater sample were determined after passing each of the five samples through the apparatus without a filter.

Results and Discussion

Filters

When we first considered looking at the possibility of femto- (0.02–0.2 μm) and picoplankton (0.2–2.0 μm) passing through 0.2-μm filters we intuitively felt that the filter would act as a true sieve, retaining all organic and inorganic particles above the stated 0.2-μm pore diameter e.g. bacteria, cyanobacterial picoplankton, nanoflagellates, etc., and passing all particles below the stated diameter, e.g. viruses and ultramicrobacteria (Daft et al. 1970; Tabor et al. 1981; Torrella and Morita 1981).

Many of the polycarbonate filters that were examined with SEM contained large pores or 'holes' of much greater diameter than the stated pore size (Fig. 1A,B). Some of the largest holes (>1 μm) were most commonly found on small ridges on the filter's surface (Fig. 1B,C). Even the lower porosity 0.2-μm Poretics® filters showed the same characteristic ridging found on Nuclepore®, but there were fewer of them (Fig. 1D). Another feature of the higher porosity 0.1 and 0.2-μm Nuclepore® filters was the close juxtaposition of several nucleation-tracks apparently fused together to form several larger pores (Fig. 1A,C). This was especially evident on the surface of the 0.1-μm filter that seemed to lack the ridging but had a greater number of fused, multiple tracks (Fig. 1A). It is unclear whether these fused tracks remain contiguous to the filter's lower surface or separate on passage through the filter, emerging on the under surface as closely spaced single pores. Because both sides of the polycarbonate filters showed large pores and photographs of filtrates from these filters show passage of large particles (>1 μm), we believe that at least some of these larger pores must remain intact to become the main source of filter leakage. As raw water passes through these 'flawed' filters, it is likely that the enlarged pores participate much more actively in the filtration process by channeling greater volumes of water through the filter, and presumably more particles as well (Brock 1983).

To allay some initial concern that we may have used a defective batch of filters we requested SEM photos of 0.2-μm nucleation-track Nuclepore® filters using another electron microscope and batch of filters from the Great Lakes Research Division, University of Michigan. Characteristics nearly identical to those shown in Fig. 1A–C (ridging, large 'holes') were observed in these micrographs (L. Sicko-Goad, Great Lakes Research Division, University of Michigan, Ann Arbor, pers. comm.).

Because polymer membranes act as true filters, not sieves, trapping particles on both the surface and within the polymer matrix (Sheldon 1972; Brock 1983), it is more difficult to assess the filter for large openings or 'holes' that would allow particles

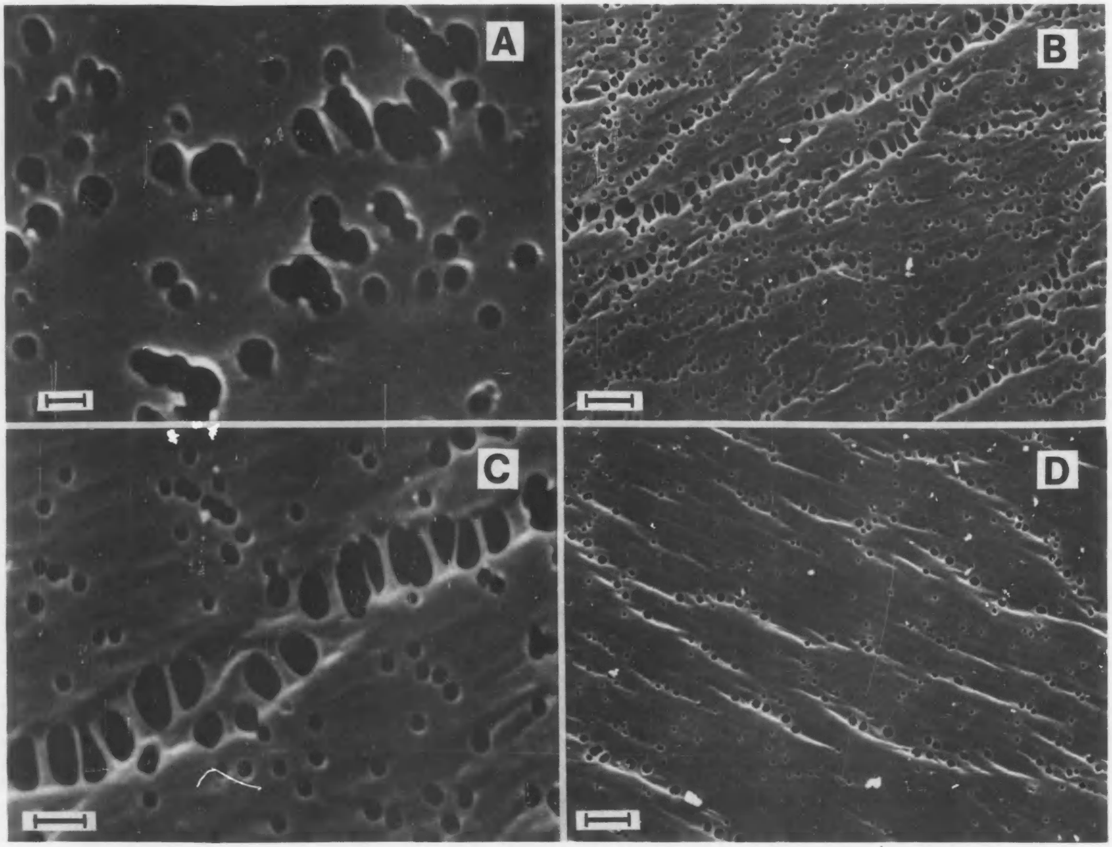

FIG. 1. Scanning electron micrographs of nucleation-track polycarbonate filters. (A) 0.1—μm Nuclepore, bar = 0.2 μm, (B) 0.2-μm Nuclepore, bar = 2 μm, (C) 0.2-μm Nuclepore, bar = 1 μm, (D) 0.2-μm Poretics, bar = 2 μm.

to pass. It has also been noted that the measured size of surface pores may bear little relation to the retention characteristics of the filter (Brock 1983). However, we noted the prevalence of large holes (>2.0 μm) on the surface of both the Millipore® type GS and Sartorius® cellulose nitrate 0.2-μm filters (Fig. 2A,B), and the occurrence of large particles in the filtrates suggests that some of these large surface pores may act as funnels for the passage of larger particles through the filter.

The Anopore® inorganic membrane filters are made by an entirely different process than nucleation-track or membrane filters (Furneaux et al. 1989), and their surface shows more uniformity both in spacing of pores and in achievement of stated nominal pore diameter, but these filters too had some larger pores or 'cracks' (Fig. 2C). Anopores® are a less flexible, more brittle filter than either polycarbonate or polymer membranes and it is possible that some of the cracks we observed occurred as a result of handling. Nonetheless they are a very high porosity filter that exhibited the most rapid filtration rate of any of the filters tested.

Vacuum

In this investigation we did not focus on the effects of varying vacuum pressure on filter retention. However, we were curious whether excessively high vacuum pressures (>150–200 mm Hg (2040–2720 Pa) would disrupt the cells and diminish retention of 0.2-μm filters. We ran several tests at vacuum pressures ranging from 50 –550 mm Hg (680–7480 Pa), and results from SEM scans of filtrates showed only a slight increase in passage of organisms through both the 0.2-μm polymer and polycarbonate filters at vacuum pressures above 300 mm Hg (4090 Pa) (we did not test the Anopore), but there were no obvious structural defects, e.g. broken cell walls, naked chloroplasts or other organelles to indicate cell damage by high vacuum pressures. Our findings were very similar to those of Li (1986) who suggested that filter retention as a function of increasing vacuum pressure appears dependent on a number of variables (e.g. cell size, density, flexibility, filter pore diameter, thickness) that can lead to highly variable results. Based on these findings we decided to use <80 mm Hg (<1090 Pa) as a routine upper limit for subsequent filter retention experiments.

Filtrates

The filtrates of 0.1 and 0.2-μm Nuclepores® obtained from Sproat Lake and Burrard Inlet samples contained a variety of organisms, including viruses, ultramicrobacteria, bacteria, phototrophic pico- and nanoplankton and some diatoms (Fig. 3A,B). Filtrates from 0.2-μm Millipore® and Sartorius® filters

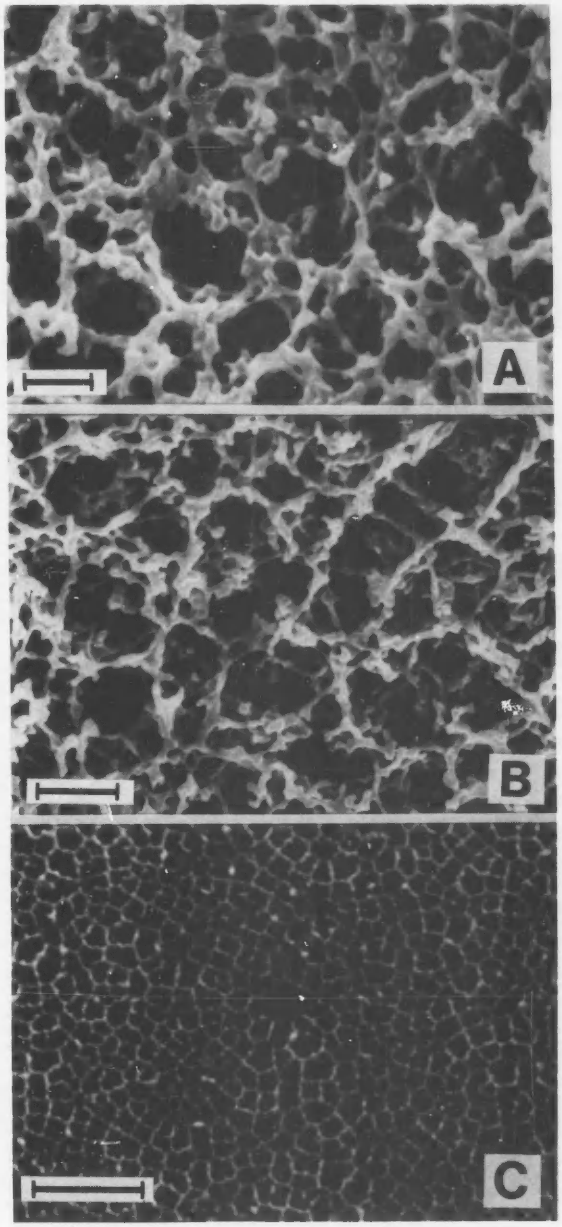

FIG. 2. Scanning electron micrographs of polymer and inorganic membrane filters. (A) 0.2-μm Millipore, bar = 4 μm, (B) 0.2 μm Sartorius, bar = 2 μm, (C) 0.2-μm Anopore, bar = 1 μm.

also contained a wide variety of organisms very similar in number and distribution to what was found in Nuclepore® and Poretics® filtrates (Fig. 3C,D). Filtrates from the 0.2 μm Anopore® filter showed some very small particles (unidentified) and a few larger cells (Fig. 3E). Though we did not verify this with quantitative procedures it was readily apparent from visual scans that both polymer and nucleation-track filters were passing similar amounts and sizes of particles but the inorganic membrane was passing less.

TEM observations provided evidence for passage of phototrophic cyanobacteria and small chlorophytes with their characteristic photosynthetic lamellae in filtrates from Sproat Lake samples (Fig. 4A,B). These observations confirmed our initial impression that some phototrophic pico- and nanoplankton were passing the 0.2-μm filters. As expected, there were greater numbers of smaller particles (range 0.4–1.0 μm) in the filtrates than larger cyanobacteria, nanoplankton, or diatoms. We were surprised to find microphytoplankton with minimum diameters from 3–7 μm in the 0.2-μm filtrates and conducted additional experiments, using several different types of filtration manifolds, to confirm that the filtrate was not contaminated with unfiltered water that may have by-passed the filter, perhaps due to a faulty seal on one of our manifolds. However, diatoms were persistently found in all 0.1 and 0.2-μm filtrates from both fresh and salt water samples, e.g. *Cyclotella* and *Rhizosolenia* and *Skeletonema* and *Coscinodiscus* (Fig. 5A–E).

Leakage

We conducted several experiments to examine the particle concentration and distribution in filtrates of the five filters tested. Initial results showed what we considered to be very high passage of particles (size range, 0.6–12.8 μm), >30% through most of the 0.2-μm filters tested. In some experiments we had to dilute samples and were uncertain whether the dilutant, particle-free seawater, was in fact particle free (Li 1989). We also were concerned about spurious counts in the lower three channels (0.6–1.0 μm) of the Coulter-Counter® (Sheldon 1979), so we repeated these earlier experiments with a more stringent protocol, using three filters of each type and examining each filtrate for particle concentrations.

The Anopore® inorganic membrane filter passed the fewest total particles (size range 1.0–12.8 μm), <3%, while the nucleation-track Poretics® passed over 14% (Table 1). Millipore® and Sartorius® filters were similar with averages of <8%, and Nuclepore® passed somewhat less — <7%. There was a total particle count in the raw, unfiltered seawater of 9.28×10^5 / mL ($n = 5$) with the Poretics® passing an average of 133×10^3 / mL and Anopore® 20×10^3 / mL. Not surprisingly, the greatest passage of particles occurred in the 1.0–1.3 μm size range (phototrophic picoplankton range) and the next greatest passage for all filters was in the size range 4.0–6.4 μm (nanoflagellate range). The filters undoubtedly passed even larger numbers of particles in the bacteria and prochlorophyte size range (<1.0 μm), but for reasons previously given we were not able to accurately assess this loss with the Coulter Counter®, but our SEM micrographs indicated that this loss did in fact occur. Clearly, for more detailed assessment of particles not retained by filters other counting instrumentation e.g. flow cytometry, should be used in future studies.

These results are not unlike those reported by Li (1986), who found a wide range of retention values using flow cytometry to look at spectral signatures of phototrophs in filtrates from a variety of filters, including the 0.1 and 0.2-μm Nuclepore® and 0.2-μm Millipore®. Jones et al. (1989) have only recently reported 21–33% higher direct bacterial counts using 0.2-μm Anopores® compared with 0.2-μm Nuclepores®, and our results would tend to support these observations. Highly variable results seem to be a disturbing but common feature of

TABLE 1. Filters used to estimate the percentage passage of all particles within the size range from 1.0–12.8 μm[a]. () = SD.

Filter	Diameter (mm)	Pore diameter (μm)	Passage (%)	Number tested
Poretics®	25	0.2	14.3 (3.98)	3
Nuclepore®	25	0.2	6.2 (0.46)	3
Millipore®	25	0.22	7.9 (1.18)	3
Sartorius®	47	0.2	7.1 (3.12)	3
Anopore®	25	0.2	2.2 (0.13)	3

[a] Total cell count of particles in the size range 1.0–12.8 μm in raw seawater sample ($n = 5$): 9.28×10^5/mL.

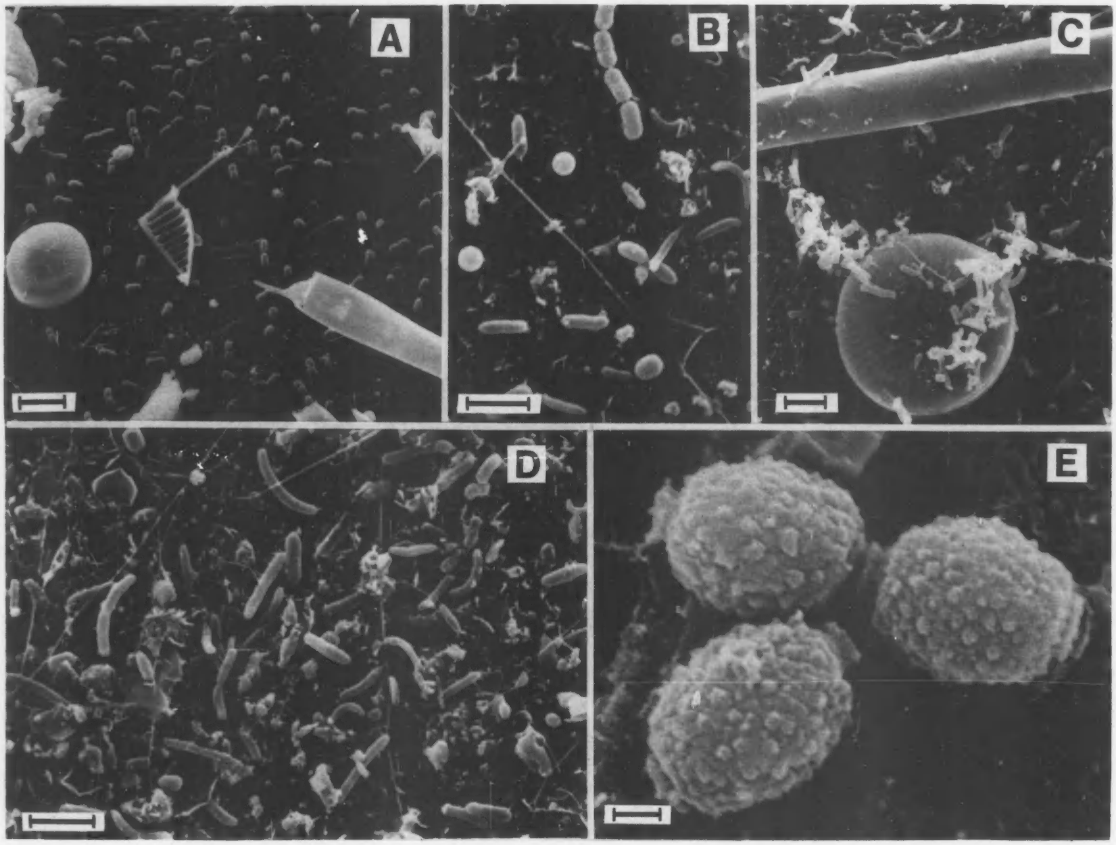

FIG. 3. Scanning electron micrographs of filtrates. (A) 0.1 μm Nuclepore, Sproat Lake, bar = 5 μm, (B) 0.2-μm Nuclepore, Sproat Lake, bar = 2 μm, (C) 0.2-μm Millipore, Sproat Lake, bar = 2 μm, (D) 0.2-μm Sartorius, Sproat Lake, bar = 2 μm, (E) 0.2-μm Anopore, Burrard Inlet, bar = 0.6 μm.

recent studies that have examined particle passage through filters (Phinney and Yentsch 1985; Li 1986; Taguchi and Laws 1988).

Implications

It is important to emphasize two points before discussing some of the implications of possible flaws in the 0.2-μm filter. The first concerns the product. There are many types of filters including glass fiber, polymer, and inorganic membrane, nucleation track, silver, etc., that are available in a wide range of nominal pore diameters (e.g. from 0.01 to 12 μm). These filters can be used on a variety of filtration equipment and researchers seem to utilize vacuum pressures that range from 0 (gravity) to 550 mm Hg (7480 Pa). Thus the filtration procedure is inherently highly variable. Product consistency in filter manufacture is also a likely source of variation, with particle retention by certain batches of filters better than others. We have noticed this in our SEM scans of filters and filtrates and consider this likely to be one of the major sources of variability both among filter types and between filters from the same package.

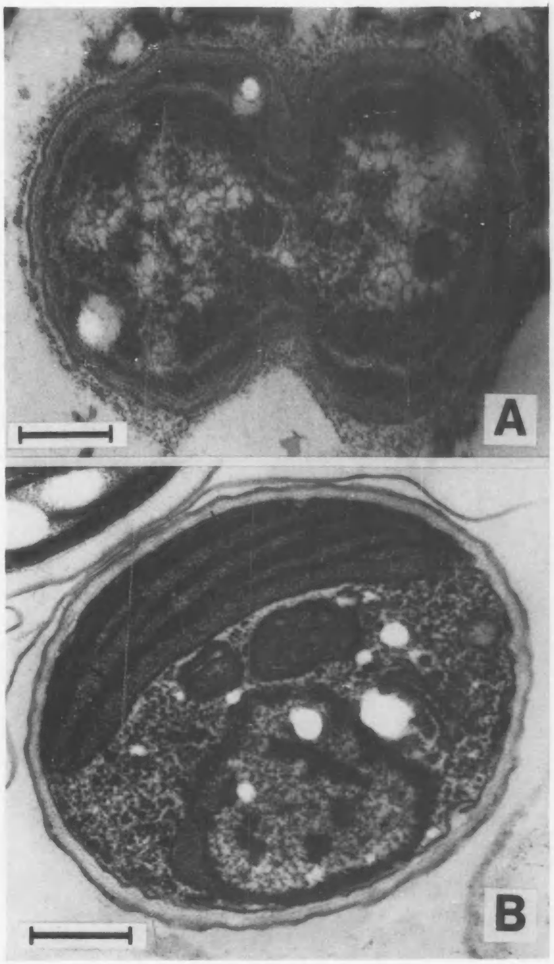

FIG. 4. Transmission electron micrographs of phototrophic picoplankton in 0.2-μm Nuclepore filtrate of Sproat Lake water. (A) Cyanobacteria, bar = 0.2 μm, Note presence of thylakoids (arrows). (B) Chlorophyte, bar = 0.4 μm.

The second point is that we consider our findings and their implications to be more applicable to studies of very oligotrophic ecosystems (e.g. tropical and subtropical oceans; large, deep temperate lakes), where small, pelagic protists are the predominant players in nutrient and carbon flux processes (Pomeroy 1974; Williams 1984; Li et al. 1983; Stockner and Antia 1986). In these dilute, nutrient impoverished waters, investigators are often forced to filter much larger quantities of water to obtain meaningful metabolic or biomass measurements and the opportunity for significant loss through 'leaky' filters is probably greatly increased.

One of the more obvious implications of 'leaky' 0.2-μm filters is the loss of bacteria and phototrophic picoplankton in the size range of 0.2–1.0 μm with the possible underestimation of production and biomass of these component organisms. Using results reported here and those provided by recent literature (Li 1986; Taguchi and Laws 1988) would suggest that this loss could be as much as 15–35% for bacteria and 5–15% for phototrophic picoplankton. However, in some size-fractionation studies, where attempts are made to separate pico- from small nanoplankton, there is the possibility that this loss of small particles through the 0.2-μm filter could be balanced by larger organisms passing through flaws in larger porosity filters (e.g. 0.6, 0.8, 1, 2, or 3 μm pore diameter), thereby exaggerating estimates of successively smaller fractions. Recent SEM examination of an 0.8-μm Nuclepore® showed ridging and several large pores similar to what we observed on the 0.2-μm Nuclepore® (Fig. 1B,C) (L. Sicko-Goad, Great Lakes Research Division, University of Michigan, Ann Arbor, pers. comm.). Thus, it is likely that this cascading effect of leakage from various filter arrays does in fact occur. We feel that this potential problem should be addressed in greater detail.

Some physiological experiments utilizing isotopes (^{15}N, ^{14}C, ^{32}P) often rely on a precise separation of either autotrophs from heterotrophs or phototrophic pico- or nanoplankton from microphytoplankton for the estimation of various kinetic parameters to be ascribed to respective groups (Derenbach and Williams 1974; Currie and Kalff 1984 a,b; Probyn and Painting 1985; Wheeler and Kirchman 1986; Chisholm et al. 1988; Wilkner and Hagstrom 1989). If leakage through the various filter arrays used for separations is not verified either microscopically or by culturing (incubation), then uptake rates could be either under- or overestimated. As suggested by Azam and Hodson (1977) and later verified by Cynar et al. (1985); Craig (1986); Taguchi and Laws (1988); and Li (1989), passage of autotrophic cyanobacteria and eucaryotic pico- and nanoplankers through 0.2, 0.4, 0.6, 1.0 μm Nuclepores® does occur, and any results obtained when using these filters as sieves to partition microorganisms must be cautiously interpreted, especially if 'clean' separations have not been verified.

Li and Dickie (1985) have warned of the implications of small, ultramicrobacteria and other protists passing 0.2-μm Nuclepores® on dilution experiments when filtered water is required for these grazing experiments. Because the 0.2-μm polymer membrane can trap particles smaller than their stated nominal pore size, these investigators suggest their use over Nuclepores®. Our own results would suggest that the polymer membranes (Millipore®, Sartorius®) and Nuclepore® were very similar and that the most effective filter may be the Anopore®. Any experiments requiring large amounts of 'sterile' water made by passage of the water through either glass fiber or membrane filters must be suspect for it will **always** contain viable femto- (0.02–0.2 μm, viruses and ultramicrobacteria) and heterotrophic and phototrophic picoplankton unless the sample has been autoclaved after filtration. This has recently been documented by flow cytometric analysis by Li (1989) who found a mixed assemblage of marine ultraphytoplankters in the filtrates from 0.2–0.45 μm nucleation-track (Nuclepore®), polymer (Millipore®) and glass-fiber (Whatman® GF/F) filters. These autotrophs were capable of rapid growth in the seawater filtrate, indicating viable, 'intact' passage through the pores of the filters tested.

Often glass-fiber (e.g. Whatman® GF/F or GF/C), Millipore®, or silver filters with nominal pore diameters of 0.4–0.7 μm are used in separating particulate from dissolved organic matter (Strickland and Parsons 1972; Gordon and Sutcliffe 1974; Johnson and Wangersky 1985). Though our study did not focus on glass-fiber filters, others have documented their poor retention characteristics (Munawar et al. 1982; Yentsch 1983; Phinney and Yentsch 1985; Taguchi and Laws 1988). Clearly the measurements of particulate carbon (C), nitrogen (N), phos-

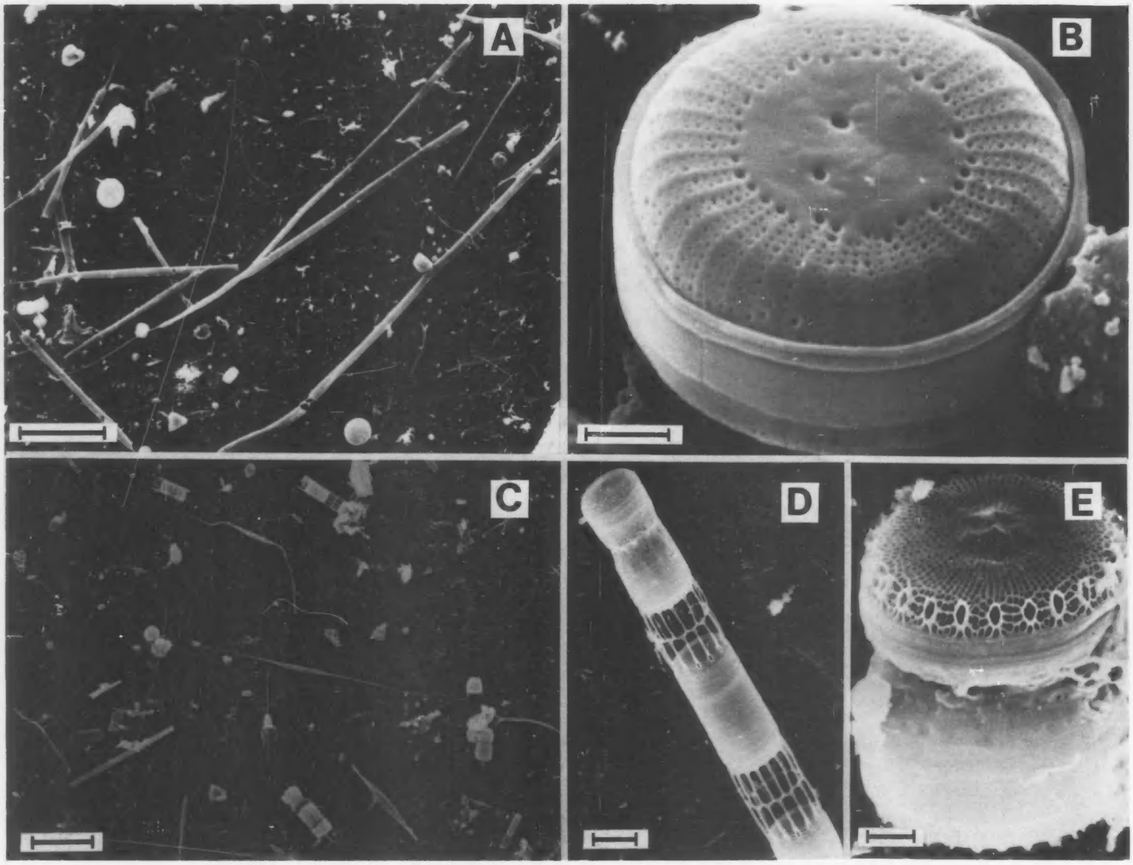

FIG. 5. Scanning electron micrographs of microphytoplankton passing 0.1 and 0.2-μm Nuclepore filters. (A) 0.1 μm filtrate, Sproat Lake, bar = 40 μm, (B) Cyclotella in 0.2-μm filtrate, Sproat Lake, bar = 1 μm, (C) 0.2-μm filtrate, Burrard Inlet, bar = 30 μm, (D) Skeletonema in 0.2-μm filtrate, Burrard Inlet, bar = 30 μm, (E) Coscinodiscus in 0.2-μm filtrate, Burrard Inlet, bar = 8 μm.

phorus (P), or chlorophyll may be underestimated by use of glass fiber or silver filters, and even 0.2-μm nucleation track or polymer membranes will pass a portion, albeit small, of the particulate matter. On the other hand values of dissolved organic carbon, nitrogen, or phosphorus or dissolved inorganic nutrients (nitrate, ammonia, phosphate, etc.) may be exaggerated by inclusion of particulate femto- and picoplankton in the filtrate. The consequences of this leakage may be trivial in meso- or eutrophic ecosystems, but much more significant in oligotrophic situations.

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A Unified Approach to the Analysis of Fish Growth, Maturity, and Survivorship Data

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This paper presents an approach to the analysis of growth, maturity, and survivorship data that unifies an extensive biometrics literature, particularly in fisheries and forestry. The model involves a probabilistic response y ($0 \leq y \leq 1$) to a positive factor x ($0 \leq x < \infty$). Because the relationship is asymptotic, the model can also be interpreted as a descriptor of biological growth, in which the asymptotic size is scaled to 1. The model generalizes earlier work by Gompertz, von Bertalanffy, Weibull, Richards, Chapman, and Schnute; it also extends the logit method introduced by Berkson. We identify reasonable curve families for the model, in which a transform parameter associated with x or y determines the curve shape, and we provide a complete analysis of curve types. We describe likelihood functions associated with two classes of data, typified by (1) size-at-maturity data and (2) time–mortality data. We illustrate the model's application to both data classes and show that it provides a useful extension to past methods of analysis.

Cet article présente une méthode d'analyse des données relatives à la période de croissance, à la période de maturité et à la survie. Cette méthode fait la synthèse de nombreux travaux en biométrie, particulièrement dans les domaines des pêches et de la foresterie. Suivant notre modèle, un facteur x ($0 \leq x\ \infty$) suscite une réponse probabiliste y ($0 \leq y \leq 1$). Comme cette relation est asymptotique, notre modèle peut également être interprété comme un modèle descriptif de la croissance biologique où l'asymptote est réduite à une échelle s'étendant jusqu'à 1. Ce modèle fait la synthèse des travaux précédents de Gompertz, von Bertalanffy, Weibull, Richards, Chapman et Schnute; il constitue aussi une extension de la méthode du logit mise au point par Berkson. Nous avons identifié des familles de courbes appropriées au modèle, dans lesquelles un paramètre de transformation associé à x ou y détermine la forme de la courbe, et nous avons fait une analyse détaillée des types de courbes. Nous avons décrit les fonctions de vraisemblance relatives aux deux classes de données suivantes : (1) données relatives à la taille et à la maturité et (2) données relatives au temps et à la mortalité. Nous donnons des exemples d'applications du modèle pour les deux classes de données et montrons en quoi cette nouvelle approche constitue une amélioration des anciennes méthodes d'analyse.

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1. Introduction

In this paper we present a unified approach to the analysis of fish growth, maturity, and survivorship data. The concepts that we discuss cover a wide variety of situations in which a response y over the range (0,1) is related to a factor x. For example, y could be the probability of death in response to the concentration x of a pollutant. Similarly, y could be fish size in relation to age x, provided that y is scaled to an asymptotic size at $y = 1$. In general, since y is defined over the finite interval (0,1) and x may range over the interval $(0,\infty)$, the model here deals with asymptotic relationships between x and y.

There are many examples of asymptotic curves in biology. Growth over time, for instance, has been studied extensively (Ricker 1975, chap. 5, 1979). The model here generalizes several popular growth models, including the classical logistic, Gompertz (1825), von Bertalanffy (1938), Richards (1959), Chapman (1961), and Schnute (1981) models. In addition, our model generalizes the Weibull (1951) distribution, frequently applied to problems in forestry. The model allows for a wide range of curve shapes, including sigmoidal curves as well as curves without inflection points. We consider increasing relationships only because the response variable for a decreasing relationship can simply be replaced by $1 - y$. For example, we consider either mortality or survivorship, whichever is an increasing function of x.

The historical literature on maturity and survivorship data is substantial. Much of the original work was directed toward dose–response and time–mortality data. These analyses typically involve a transformation η to map the probability interval (0,1) onto the real line $(-\infty,\infty)$. One commonly used transform is the logit

$$(1.1) \quad \eta = -\ln(y^{-1} - 1),$$

introduced by Berkson (1944, 1951) and surveyed by Ashton (1972). The probit transform, introduced by Bliss (1934), is

$$(1.2) \quad \eta = \Phi^{-1}(y)$$

where Φ represents the standard normal cumulative distribution function

$$\Phi(\eta) = (2\pi)^{-1/2} \int_{-\infty}^{\eta} e^{-w^2/2} dw.$$

Probit analysis was first used to estimate size-at-maturity by Leslie et al. (1945) and has since become a widely accepted method (e.g. Finney 1971). For a more recent fisheries example based on a different analysis, see Welch and Foucher (1988).

The modern analytical theory is described succinctly by McCullagh and Nelder (1983, chap. 4). Our presentation has features in common with theirs. We emphasize the interrelationships between x and y via their corresponding transforms ξ and η. These interrelationships may be illustrated as

$$(1.3) \quad x \leftrightarrow \xi \leftrightarrow \eta \leftrightarrow y.$$

Here, ξ and η act as surrogates of x and y, to which they are nonlinearly related, and η is linearly related to ξ. For example, ξ may represent an exponential transform (Box and Cox 1964) of x,

$$(1.4) \quad \xi = (x^c - 1)/c,$$

dependent on the parameter c. Transforms (1.1), (1.2), and (1.4) differ from the ones we discuss below, but they serve here to illustrate the concepts.

The probit and logit transforms are somewhat restrictive, as both are symmetric around $y = 0.5$, where $\eta = 0$. We use a more general transform η adapted from Schnute and Jensen (1986, equation (2.15)). This transform contains an extra parameter to allow for asymmetry, and it includes the logit transform as a special case. There are, in fact, four parameters in our complete model. Two of these are exponents used for the x and y transforms and two parameters essentially describe the linear relationship between η and ξ. We recognize that this model is overparameterized, but we wish to provide the user with maximum flexibility and to encompass as much of the historical literature as possible. We investigate families of curves that result from fixing the transform parameters and discuss suggestions for tailoring the model to specific applications.

As an alternative to earlier methods, such as that of Welch and Foucher (1988), our model has several distinct advantages. It includes numerous historical models as special cases. It allows for a wide range of curve types, with various degrees of skewness. The curves are not forced to $y = 0$ or $y = 1$ necessarily. It is self-consistent for various measures of the factor x. For example, if weight w is proportional to the cube of length l, then consistent parameter estimates are obtained using either w or l^3 as the factor x. Finally, the model can be formulated in a way that focuses on the parameters of principal interest, such as size at 50% maturity or dose for 50% mortality.

Logically, the paper begins by defining a curve family that encompasses a broad range of fisheries and forestry literature. After investigating deterministic properties of this family, we next discuss its statistical application. In particular, we present likelihood functions appropriate in specific contexts. Although we do not consider growth model likelihoods (which are relatively straightforward), we provide an overview of methods traditionally associated with studies of maturity and survivorship.

Data from such studies can be divided into two fundamentally different classes. First, consider a sample of fish for which the size of each fish is measured and the fish is determined to be mature or immature. The data for fish i then consist of its size x_i and maturity status u_i, where u_i is a binary variable that takes the value 0 if the fish is immature or 1 if the fish is mature. In contrast, consider an experiment in which fish are exposed to a lethal concentration of a toxicant. The data for fish i then consist simply of x_i, the time of death. Bliss (1937, p. 816) suggested that the analysis of time–mortality data is, in fact, simpler than the corresponding analysis of dose–response data. In modern terms, the essential difference between these analyses comes from the different likelihood functions for each case. We show that (given modern computing technology) they pose problems of comparable difficulty.

TABLE 1. Special cases of the model (2.1) for various values of the parameters b and c. In cases marked with an asterisk, comparison with the historical model assumes that y is scaled in units of y_∞, where y_∞ is the asymptotic size. See the discussion in connection with (2.15).

b	c	Description
−1	1	von Bertalanffy*
0	1	Gompertz*
1	0	Logit–log
1	1	Logistic,* logit–linear
−1	Free	Weibull
1	Free	Logit–exponential
Free	0	Generalized logit–log
Free	1	Richards,* Chapman,* Schnute,* generalized logit–linear

Section 2 of this paper develops the model from three different perspectives: historical, conceptual, and computational. Section 3 describes the model's properties, both analytically and graphically. Section 4 examines special cases that result from restricting the transforms $\xi(x)$ and $\eta(y)$ in (1.3). We identify curve families in which one transform parameter is fixed and the other serves to determine curve shape. Our analysis suggests reasonable procedures for choosing an appropriate model for a given context. In Section 5, we present likelihood functions and parameter estimation techniques for the two classes of data. Finally, in Section 6, we provide worked examples for both size-at-maturity and time–mortality data sets. In each example, we obtain confidence regions for the model parameters, with particular emphasis on the parameters of greatest practical interest.

In order to give perspective to the model's technical details, we defer mathematical proofs to appendices, and we often compile equations into tables. We use parentheses and brackets, respectively, to distinguish equations in the text from those in tables. For example, "(2.4)" and "[2.4]" indicate the fourth equation in Section 2 and Table 2, respectively.

2. The Model

In this section we present three equivalent formulations of the model. The first relates to the model's historical context, the second to its conceptual framework, and the third to its numerical formulation. Because of its connection with the general linear model (McCullagh and Nelder 1983), we ultimately use the third version for most analyses in this paper.

To state the first version of the model, let y $(0 \leq y \leq 1)$ be the probabilistic response to a positive factor x. Then the model consists of the equation

$$(2.1) \quad y^{-b} = 1 + \alpha e^{-ax^c}$$

with four parameters a, b, c, and α. For example, if $b = c = 1$, then (2.1) is the classical logistic relationship

TABLE 2. Model equations formulated for theoretical and computational purposes. The relationships (1.3) among x, ξ, η, and y are expressed in terms of constants (β, f, g) determined by the model parameters. The model derivatives ($z = dy/dx$, $\zeta = d^2y/dx^2$) and two critical values of η (η', η'') are also shown. Where appropriate, the table includes the limiting version of each equation as $b \rightarrow 0$ or $c \rightarrow 0$.

[2.1a]	β	=	$\ln[(y_1^{-b}-1)/(y_2^{-b}-1)]$;	$b \neq 0$
[2.1b]	β	=	$\ln[\ln(y_1)/\ln(y_2)]$;	$b=0$
[2.2a]	f	=	$c/[(x_2/x_1)^{c}-1]$;	$c \neq 0$
[2.2b]	f	=	$1/\ln(x_2/x_1)$;	$c=0$
[2.3a]	g	=	$(y_1^{-b}-1)/b$;	$b \neq 0$
[2.3b]	g	=	$-\ln(y_1)$;	$b=0$
[2.4a]	ξ	=	$(f/c)\cdot[(x/x_1)^c-1]$;	$c \neq 0$
[2.4b]	ξ	=	$f\cdot\ln(x/x_1)$;	$c=0$
[2.5]	η	=	$\beta\xi$	
[2.6a]	y	=	$[1+bge^{-\eta}]^{-1/b}$;	$b \neq 0$
[2.6b]	y	=	$y_1^{(e^{-\eta})}$;	$b=0$
[2.7a]	x	=	$x_1\cdot[1+(c/f)\xi]^{1/c}$;	$c \neq 0$
[2.7b]	x	=	$x_1\cdot(x_2/x_1)^{\xi}$;	$c=0$
[2.8]	ξ	=	η/β	
[2.9a]	η	=	$\ln[bg/(y^{-b}-1)]$;	$b \neq 0$
[2.9b]	η	=	$\ln[\ln(y_1)/\ln(y)]$;	$b=0$
[2.10a]	z	=	$(\beta f/x_1)\cdot(x/x_1)^{c-1}\cdot[(1-y^b)/b]\cdot y$;	$b \neq 0$
[2.10b]	z	=	$(\beta f/x_1)\cdot(x/x_1)^{c-1}\cdot ge^{-\eta}\cdot y$;	$b=0$
[2.11]	ζ	=	$-(y^b z/x)\cdot e^{-\eta}\cdot H(\eta)$	
[2.12]	$H(\eta)$	=	$(c\eta+\beta f)(e^{\eta}-g) + (1-c)(e^{\eta}+bg)$	
[2.13]	η'	=	$-\beta f/c$;	$c \neq 0$
[2.14]	η''	=	$\ln(-bg)$;	$b<0$

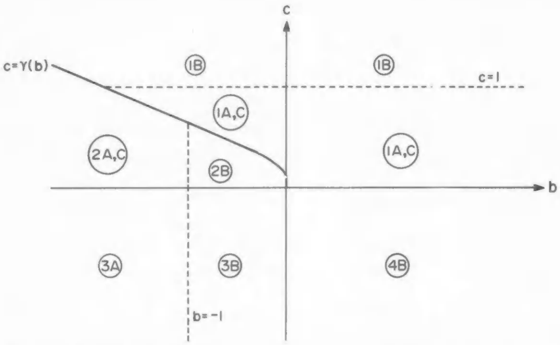

FIG. 1. Curve types in bc-space with (x_1,y_1) and (x_2,y_2) fixed. The broken line parallel to the b-axis is defined by $c = 1$, and the broken line parallel to the c-axis is defined by $b = -1$. The curved line corresponds to $\gamma(b)$ in (3.3).

$$(2.2)\quad y = \frac{1}{1 + \alpha e^{-ax}}$$

(Ricker 1975, p. 310–315) with an asymptote at $y = 1$. More generally, as summarized in Table 1, (2.1) corresponds to various historical relationships determined by choices of the parameters b and c. In particular, the choice $b = -1$ leads to the Weibull (1951) distribution, which has been extensively applied in forestry literature (Bailey and Dell 1973; Schreuder and Swank 1974; Stauffer 1979). Similarly, the choice $c = 1$ underlies popular asymptotic curves in fisheries and other biological literature (Gompertz 1825; von Bertalanffy 1938; Chapman 1961; Richards 1959; Schnute 1981). Because the model (2.1) includes all these historical models as special cases, it provides a unified analytical framework for a diverse literature.

The second formulation of our model emphasizes two points on the curve (2.1). As suggested by G. Evans (pers. comm.), the relationship between x and y implicitly defined by

$$(2.3)\quad \frac{G(y) - G(y_1)}{G(y_2) - G(y_1)} = \frac{F(x) - F(x_1)}{F(x_2) - F(x_1)}$$

passes through the points (x_1,y_1) and (x_2,y_2) for arbitrary monotone functions $F(x)$ and $G(y)$. To relate (2.3) to (2.1), let

$$(2.4)\quad F(x) = \begin{cases} (x^c - 1)/c; & c \neq 0 \\ \ln(x); & c = 0 \end{cases}$$

and

$$(2.5)\quad G(y) = \begin{cases} -\ln[(y^{-b} - 1)/b]; & b \neq 0 \\ -\ln[-\ln(y)]; & b = 0. \end{cases}$$

Note that for $x > 0$, $F(x)$ is a strictly increasing function that depends continuously on the parameter c ($-\infty < c < \infty$). Similarly, when $0 < y < 1$, $G(y)$ is strictly increasing and depends continuously on b ($-\infty < b < \infty$). Furthermore, the relationship between y and x implied by (2.3)–(2.5) is equivalent to (2.1) with

$$(2.6)\quad \ln(\alpha) = \frac{x_2^c\cdot\ln(y_1^{-b} - 1) - x_1^c\cdot\ln(y_2^{-b} - 1)}{x_2^c - x_1^c}$$

and

$$(2.7)\quad a = \frac{\ln(y_1^{-b} - 1) - \ln(y_2^{-b} - 1)}{x_2^c - x_1^c}.$$

In summary, equations (2.3)–(2.5) define the second version of our model, determined by two points ((x_i,y_i), $i = 1,2$) and two transforms ($F(x)$, $G(y)$). From a historical perspective, $F(x)$ is the Box–Cox (1964) exponential transform (1.4), and $G(y)$ generalizes the logit, since (2.5) reduces to (1.1) when $b = 1$. Various possible models are identified in Table 1, according to the transforms indicated by the parameters b and c. For example, the model with $b = c = 1$ is called "logit–linear" because it results from a logit transform of y and a linear transform of x. Similarly, when $b = 1$ and $c = 0$, the model is termed "logit–log."

We obtain the third version of our model by writing (2.3) in the form

$$(2.8)\quad \eta = \beta\xi$$

where

$$\eta = G(y) - G(y_1)$$

$$\beta = G(y_2) - G(y_1)$$

$$\xi = \frac{F(x) - F(x_1)}{F(x_2) - F(x_1)}.$$

It follows from the definitions of η, β, and ξ that

(2.9) $\eta = \ln\left[\frac{y_1^{-b}-1}{y^{-b}-1}\right]$

(2.10) $\beta = \ln\left[\frac{y_1^{-b}-1}{y_2^{-b}-1}\right]$

(2.11) $\xi = \frac{x^c - x_1^c}{x_2^c - x_1^c}$.

Thus, equations (2.8)–(2.11) are equivalent to both (2.3)–(2.5) and (2.1). Our notation in (2.8) is analogous to that used by McCullagh and Nelder (1983) for describing the general linear model. Here, ξ is a transform of x, $\beta\xi$ is a linear predictor, and the relationship (2.9) between η and y defines a link function. To preserve this analogy and to obtain numerically stable equations, we apply (2.8)–(2.11) throughout the remainder of this paper.

To understand the use of equations (2.8)–(2.11), suppose that the six quantities b, c, x_1, x_2, y_1, and y_2 are all known, subject to the constraints

(2.12a) $0 < y_1 < y_2 < 1$

(2.12b) $0 < x_1 < x_2$.

The basis for the model is the set of interrelationships (1.3). The transform (2.11) defines the connection between x and ξ. Similarly, (2.10) defines a coefficient β that determines the linear relationship (2.8) between ξ and η. Finally, (2.9) determines the connection between η and y. Any one of the four quantities ξ, η, x, or y determines the other three. In particular, x and y may be obtained from ξ and η by their inverses:

(2.13) $x = [(1-\xi)x_1^{\,c} + \xi x_2^{\,c}]^{1/c}$

(2.14) $y = [1 + (y_1^{\,-b} - 1)e^{-\eta}]^{-1/b}$.

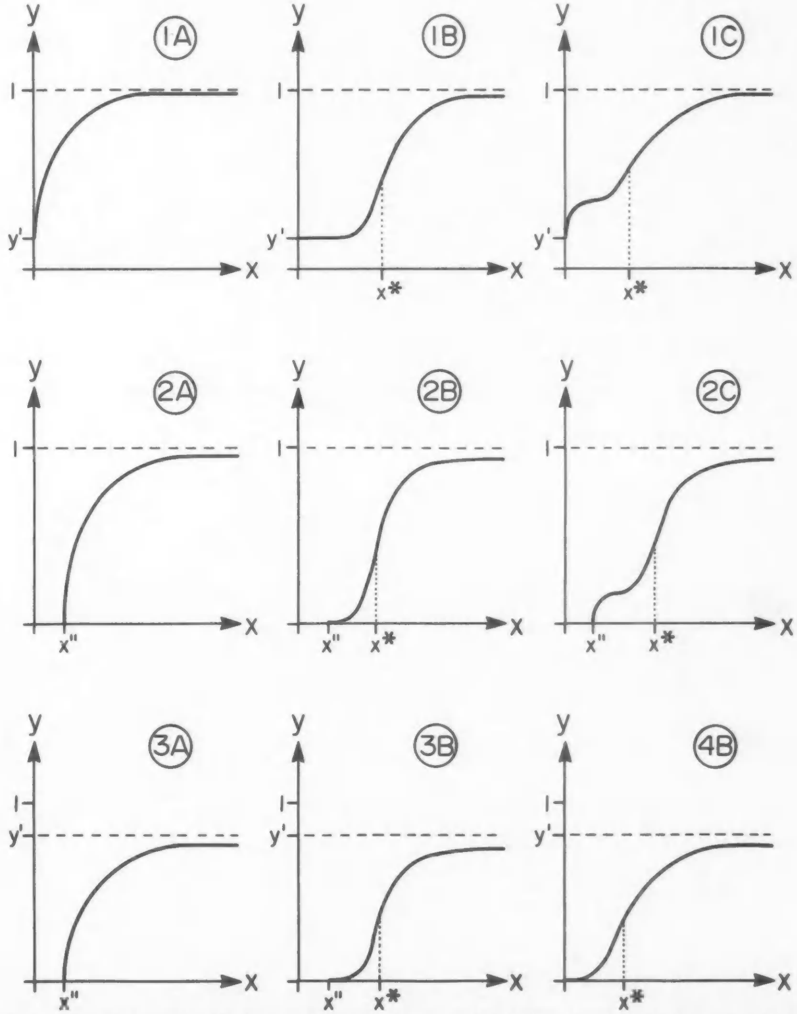

FIG. 2. Typical forms for the nine possible types of curves $y(x)$. Broken lines indicate the y-asymptote, and dotted lines show the position of an inflection point at x^*, where it exists. The effect of two inflection points has been exaggerated for curve types 1C and 2C.

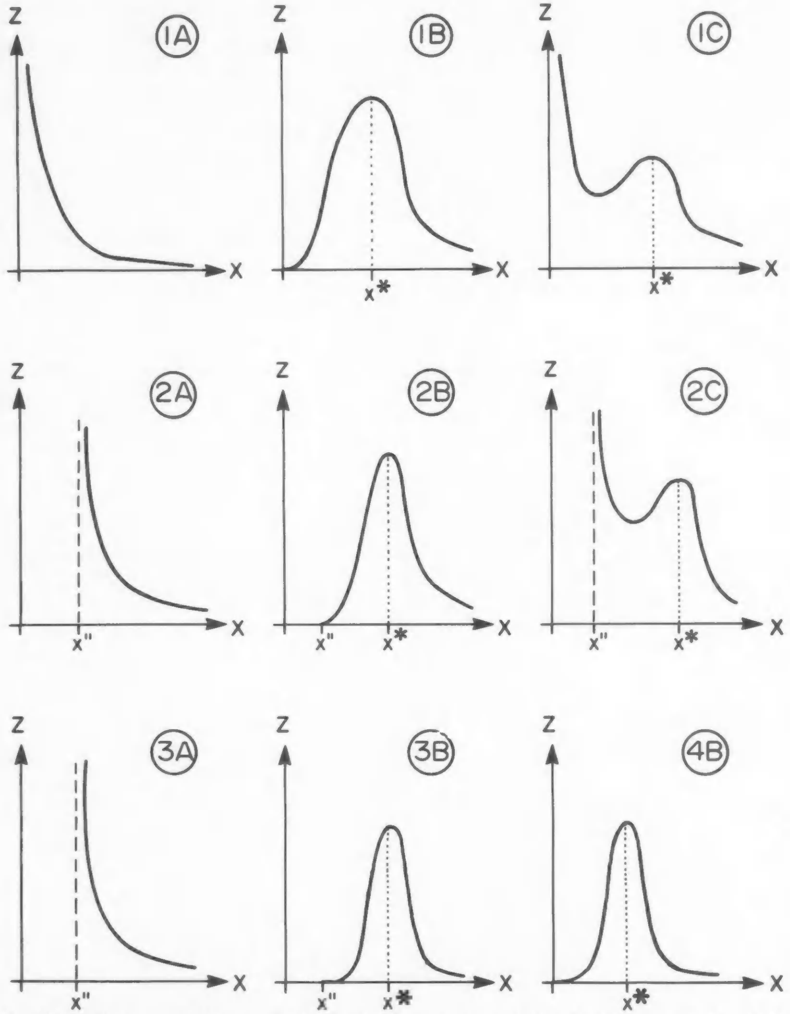

FIG. 3. Density curves $z(x)$ corresponding to the nine curve types in Fig. 2. Where appropriate, broken and dotted lines indicate an x-asymptote at x'' and a mode at x^*, respectively.

TABLE 3. Ranges of x, ξ, η, and y for the four main curve types, along with the location of curve types in the (b,c) coordinate system. The symbol 2+ indicates the region in quadrant 2 where $c>\gamma(b)$; similarly, 2− indicates the region where $c<\gamma(b)$.

Curve type	Quadrant in *bc*-space	x range	ξ range	η range	y range
1	1, 2+	$(0,\infty)$	(ξ',∞)	(η',∞)	$(y',1)$
2	2−	(x'',∞)	(ξ'',∞)	(η'',∞)	$(0,1)$
3	3	(x'',∞)	(ξ'',ξ')	(η'',η')	$(0,y')$
4	4	$(0,\infty)$	$(-\infty,\xi')$	$(-\infty,\eta')$	$(0,y')$

Thus, if x is given, then (2.11), (2.8), and (2.14) determine ξ, η and y, respectively. In particular, the reader can verify that the value x_1 determines $\xi = 0$, $\eta = 0$, and $y = y_1$. Similarly, when $x = x_2$, then $\xi = 1$, $\eta = \beta$, and $y = y_2$. The constraints (2.12) ensure that the relationship is increasing, as discussed in the Introduction.

Although the model (2.8)–(2.11) apparently contains six parameters (b,c,x_1,x_2,y_1,y_2), two of them are redundant. Either (x_1,x_2) or (y_1,y_2) must be specified in advance by the user, according to quantities of interest. For example, if the user

TABLE 4. Curve types, in relation to b, when $c=0$. Since the line $c=0$ forms a boundary between regions in Fig. 1, the resulting curve types can be variants of those shown in Fig. 2 and 3.

Condition	Type
$b \geq 0$	4B with $y'=1$; 1B with $y'=0$
$-1<b<0$	2B; 3B with $y'=1$
$b=-1$	2A with z discontinuous (but bounded) at x''
$b<-1$	2A; 3A with $y'=1$

wishes to estimate the two doses for which mortality is 20 and 80%, then appropriate choices are $y_1 = 0.2$ and $y_2 = 0.8$, respectively. From this point of view, y_1 and y_2 are presumed to be specified quantities and the four unknown parameters are b, c, x_1, and x_2. Alternatively, to estimate probabilities of mortality associated with certain toxicant levels, values of x_1 and x_2 could be specified. The model's four parameters would then be b, c, y_1, and y_2. We use the parameter set (b,c,x_1,x_2) in our discussion below, as we believe it to have the most general applicability. Incidentally, Schnute (1981), Schnute and McKinnell (1984), and Schnute and Jensen (1986) used similar concepts in their model formulations.

We have motivated our discussion with (2.1), an equation that bears obvious similarity to various classical growth models. One difference, however, is that classical models typically have an extra parameter y_∞ that represents a theoretical maximum size. If we assume that

$$(2.15) \quad y_\infty = 1,$$

then, when $c = 1$, our model is identical to Schnute's (1981) growth model with the sign of b reversed. In particular, Schnute's model includes a parameter "a" corresponding to "a" in (2.1), and the requirement (2.15) for Schnute's model determines the value "a" given by (2.7) (see Schnute 1981, equation (25)).

In relation to growth curves, our model implicitly assumes that y is scaled in units of y_∞. If we explicitly included a scale factor y_∞, the resulting five-parameter model would generalize families of growth models used in the fisheries and forestry literature. Although we do not provide a complete discussion of this extended family, most of the necessary groundwork appears in the next section. All our results can be generalized readily to include the factor y_∞. The full five-parameter family, however, also contains nonasymptotic curves (similar to those in Schnute 1981) that are not described here.

3. Model Properties

Having developed the model (2.8)–(2.12) from historical considerations, we now proceed to investigate its properties. First, from an analytical point of view, we present equations for implementing the model on a computer and for calculating its first and second derivatives

$$(3.1) \quad z = dy/dx$$

and

$$(3.2) \quad \zeta = d^2y/dx^2.$$

Second, from a graphical point of view, we identify nine possible curve types dependent on (i) the ranges of x and y and (ii) the existence of zero, one, or two inflection points.

TABLE 5. Slope of the curve $y(x)$ at the axis intercept for each of the model's curve types. The slope is either 0 or ∞, depending on various conditions for b and c.

Type	Intercept	Condition	Slope
1	$(0,y')$	$c>1$	0
1	$(0,y')$	$c<1$	∞
2	$(x'',0)$	$b>-1$	0
2	$(x'',0)$	$b<-1$	∞
3	$(x'',0)$	$b>-1$	0
3	$(x'',0)$	$b<-1$	∞
4	$(0,0)$	None	0

3A. Analytical Properties

The model's theory and application require expressions for the derivatives (3.1)–(3.2). In particular, notice that $z(x)$ represents a probability density function corresponding to a cumulative probability $y(x)$. Likelihood functions defined below depend on both $y(x)$ and $z(x)$. Furthermore, $\zeta(x)$ plays a key role in the analysis because the condition $\zeta(x) = 0$ determines an inflection point for $y(x)$ and a mode for $z(x)$.

Although the calculus is somewhat tedious, $z(x)$ and $\zeta(x)$ can be computed analytically. The results are shown in Table 2, which contains a complete set of equations for implementing the model (2.8)–(2.11). Logically, equations [2.1]–[2.3] define three constants β, f, and g determined by the parameters (b,c,x_1,x_2,y_1,y_2). These constants are used in [2.4]–[2.6] to determine the linkages $x \rightarrow \xi \rightarrow \eta \rightarrow y$; similarly, [2.7]–[2.9] give the reverse linkages $x \leftarrow \xi \leftarrow \eta \leftarrow y$. Formulas for z and ζ are given in [2.10]–[2.11], where the latter involves a function $H(\eta)$ defined by [2.12]. Finally, [2.13]–[2.14] determine two critical values of η, η', and η'', whose significance is described below. Incidentally, the prime and double prime provide convenient indicators to these special values and do not denote derivatives in this paper.

Note that equations [2.10]–[2.11] for z and ζ take account of the linkages (1.3). Thus, to calculate z from x, one first obtains the values of η and y associated with x and then computes z from [2.10]. Similarly, in order to calculate ζ, it is necessary first to obtain η, y, and z from x and then to apply [2.11]–[2.12].

Each equation in Table 2 has a finite limit as b or c tends to 0. Where this limit is indeterminate (e.g. f tends to 0/0 as $c \rightarrow 0$ in [2.2a]), the limiting form is also shown. Furthermore, the computations implied by Table 2 frequently involve the use of a power function u^v. This should be implemented as in Appendix C, both to avoid numerical errors and to truncate y-values properly in the interval [0,1].

The equations in Table 2 are either definitions ([2.2]–[2.3], [2.12]–[2.14]) or consequences of the assumed model (2.8)–(2.11). Appendix A gives proofs of these results, where required. A number of intuitive features are evident in Table 2. For example, since y is a dimensionless probability, all quantities in the table are dimensionless, except for x, x_1, x_2, z, and ζ. The parameters x_1 and x_2 have the same units as x; also, the first and second derivatives z and ζ must have units of x^{-1} and x^{-2}, respectively. The reader can verify the dimensionality of z and ζ by taking note of the factors $\beta f/x_1$ and $y^b z/x$ in [2.10] and [2.11], respectively. Similar dimensional arguments can be applied to each equation in the table. Furthermore, given the constraints (2.12), it can be shown that β, f, and g are all positive, regardless of the sign of b or c. This shows that z in [2.10] is positive, since $(1-y^b)/b > 0$ when $0 < y < 1$. Thus, the

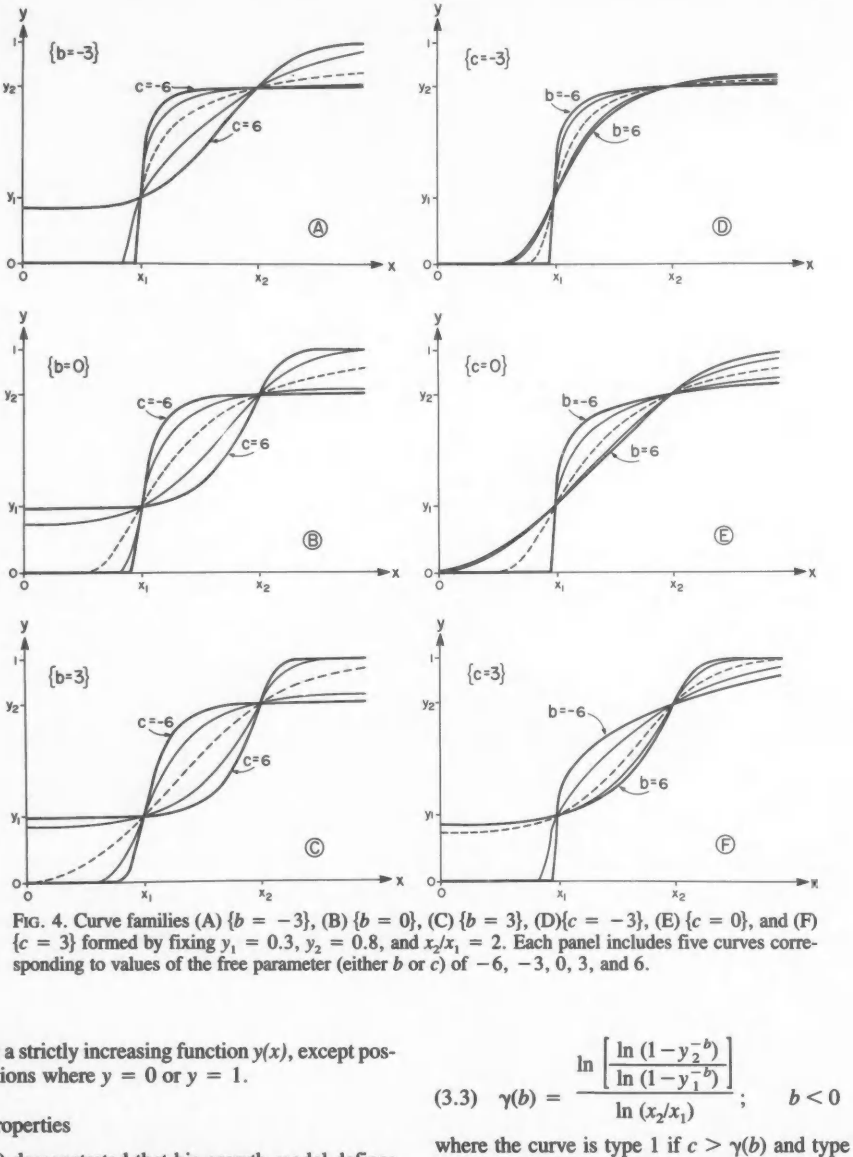

FIG. 4. Curve families (A) $\{b = -3\}$, (B) $\{b = 0\}$, (C) $\{b = 3\}$, (D)$\{c = -3\}$, (E) $\{c = 0\}$, and (F) $\{c = 3\}$ formed by fixing $y_1 = 0.3$, $y_2 = 0.8$, and $x_2/x_1 = 2$. Each panel includes five curves corresponding to values of the free parameter (either b or c) of -6, -3, 0, 3, and 6.

constraints imply a strictly increasing function $y(x)$, except possibly for flat sections where $y = 0$ or $y = 1$.

3B. Graphical Properties

Schnute (1981) demonstrated that his growth model defines a curve family with various distinct curve types. Figures 1–3 present similar results for the model (2.8)–(2.12). Four curve types (designated by a numeral 1 to 4) are possible, with up to three variants (designated by a letter A to C). Although this notation suggests a total of $4 \times 3 = 12$ types, only 9 occur. Figure 1 describes the location of each type in bc-space. Typical curve types are illustrated in Fig. 2, and the corresponding density curves from the first derivative z are presented in Fig. 3.

As illustrated in Fig. 1, curve types are primarily defined by the two parameters b and c, where type 1 is associated with the first and second quadrants of bc-space, type 2 with the second quadrant, type 3 with the third quadrant, and type 4 with the fourth quadrant. Types 1 and 2 are separated in the second quadrant by a critical c-value

$$(3.3) \quad \gamma(b) = \frac{\ln\left[\dfrac{\ln(1-y_2^{-b})}{\ln(1-y_1^{-b})}\right]}{\ln(x_2/x_1)}; \qquad b<0$$

where the curve is type 1 if $c > \gamma(b)$ and type 2 if $c < \gamma(b)$. Notice in this case that the curve type depends on (x_1,y_1) and (x_2,y_2), as well as the parameters b and c.

As illustrated in Fig. 2, the curve type relates to possible x- and y-intercepts and the location of the y-asymptote. Curves of type 1 intercept the y-axis at $y = y'$ and have an asymptote at $y = 1$. Curves of type 2 intercept the x-axis at $x = x''$ and have an asymptote at $y = 1$. Curves of type 3 have an x-intercept at $x = x''$ and an asymptote at $y = y'$. The type 4 curve arises from the origin and has an asymptote at $y = y'$. The quantities x'' and y' in this discussion have simple biological interpretations. Consider, for example, an analysis of size-at-maturity data. If the result is a type 1 curve, the implication is that a fraction y' of fish is initially mature. Alternatively, a type 2 or 3 curve would indicate a minimum size x'' at which fish first begin to mature. The asymptote for a type 3 or 4 curve implies

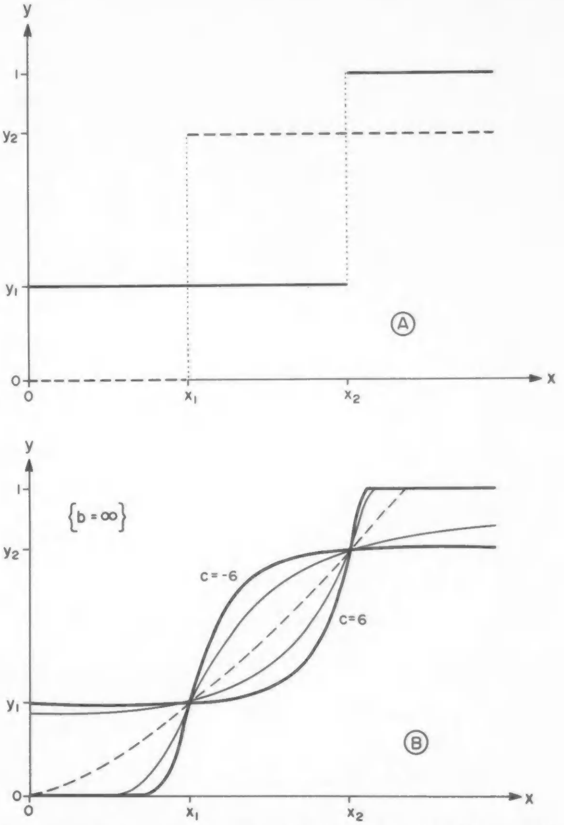

FIG. 5. (A) Extreme cases of curve families $\{b = -\infty\}$ and $\{c = -\infty\}$ (broken line) and $\{c = +\infty\}$ (solid line). Dotted lines indicate discontinuities. (B) The curve family $\{b = +\infty\}$, with parameter values corresponding to those used in Fig. 4.

that a fraction 1-y' of fish never mature, as, for example, when a parasite suppresses the attainment of sexual maturity.

Values of y' and x'' are determined by the quantities η' and η'' given in [2.13]–[2.14]. Thus, where they exist, corresponding values x', y', and ξ' may be obtained from η', and, similarly, values x'', y'', and ξ'' may be obtained from η''. Notice that the value y' could represent either a y-intercept (type 1) or a y-asymptote (types 3 and 4). These distinctions are further clarified by the ranges of x, ξ, η, and y for the four main curve types presented in Table 3. For example, the y-range extends over the interval $(y',1)$ for type 1 and over the interval $(0,y')$ for types 3 and 4.

Proofs of the existence of the curve types described here are given in Appendix B. In addition to the four main curve types, there are three possible variants, A, B, and C, corresponding to curves with 0, 1, or 2 inflection points, respectively. As indicated in Fig. 1, type B is separated from types A and C in bc-space by the lines $b = -1$ and $c = 1$ and the curve $\gamma(b)$. There are nine possible curve types in total, corresponding to 1A–C, 2A–C, 3A–B, and 4B. In practice, curves of type C are often difficult to distinguish from types A and B, as one or both of the inflection points tend to be close to the axis intercept. We have exaggerated the effect of the inflection points in Fig. 2 and 3 so that the distinctions are more evident to the reader.

TABLE 6. Curve families $\{b = \pm\infty\}$ and $\{c = \pm\infty\}$. With the exception of $\{b = +\infty\}$, each family degenerates to a single discontinuous curve. Complete defining equations for the family $\{b = +\infty\}$ are given, including expressions for the derivatives z and ζ. Neither β nor η is defined when $b = +\infty$, but relationships (1.3) among x, ξ, and y still exist. In particular, f is still defined by [2.2], and the relationship between ξ and x is still governed by [2.4] and [2.7]. Like f, the constants h, ξ_m, and ξ' are determined by model parameters.

$$\{c = -\infty\},\ \{b = -\infty\}$$

$$[6.1]\quad y(x) = \begin{cases} 0; & 0 \leq x < x_1 \\ y_1; & x = x_1 \\ y_2; & x > x_1 \end{cases}$$

$$\{c = +\infty\}$$

$$[6.2]\quad y(x) = \begin{cases} y_1; & 0 \leq x < x_2 \\ y_2; & x = x_2 \\ 1; & x > x_2 \end{cases}$$

$$\{b = +\infty\}$$

$$[6.3]\quad h = f \cdot \ln(y_2/y_1)$$

$$[6.4]\quad \xi_m = 1/[1 - \ln(y_2)/\ln(y_1)]$$

$$[6.5]\quad y = \begin{cases} y_1 \cdot (y_2/y_1)^{\xi}; & \xi < \xi_m \\ 1; & \xi \geq \xi_m \end{cases}$$

$$[6.6]\quad z = \begin{cases} (h/x_1) \cdot (x/x_1)^{c-1} \cdot y; & x < x_m \\ 0; & x \geq x_m \end{cases}$$

$$[6.7]\quad \zeta = \begin{cases} (z/x) \cdot [h(x/x_1)^{c} + c - 1] & x < x_m \\ 0; & x \geq x_m \end{cases}$$

$$[6.8]\quad \xi' = -f/c; \qquad c \neq 0$$

Density curves in Fig. 3 are obtained from z in [2.10]. All these curves asymptotically approach the x-axis as $x \to \infty$, and types A and C have an additional asymptote parallel to the y-axis. Types B and C are modal. Type C curves have two critical points, a minimum corresponding to the first inflection point in Fig. 2 and a maximum corresponding to the second. Inflection points in Fig. 2 correspond to zeros of the second derivative ζ, that is, by [2.11]–[2.12], to roots of $H(\eta)$. Since $H(\eta)$ may have 0, 1, or 2 roots (Appendix B), up to two inflection points may exist. Typically, however, only the inflection point closest to the y-asymptote is of interest. If $\eta_1{}^*$ and $\eta_2{}^*$ denote the two roots of $H(\eta)$, when they exist, then depending on the sign of c,

$$(3.4)\quad \eta^* = \begin{cases} \max(\eta_1^*, \eta_2^*); & c > 0 \\ \min(\eta_1^*, \eta_2^*); & c < 0 \end{cases}$$

is the value of η that determines the relevant inflection point (Appendix B). In Fig. 3, this point corresponds to the mode of a type B curve or to the upper mode of a type C curve.

Consistent with earlier notation, we define $x_i{}^*$, $\xi_i{}^*$, and $y_i{}^*$ $(i = 1,2)$ to be quantities corresponding to $\eta_i{}^*$, if they exist. Similarly, x^*, ξ^*, and y^* correspond to η^*. Unfortunately, analytical expressions for all of these quantities are not possible, except in certain special cases. These are discussed in the next section, where formulas for some of the quantities are provided.

We complete this section with two final comments on the analysis of curve types. First, the illustrations in Fig. 2 and 3 correspond to the interiors of the regions in *bc*-space shown in Fig. 1. On boundaries between these regions, somewhat different curve forms are possible. For example, Table 4 describes the possible curve types when $c = 0$. Regardless of the value of b, a curve with $c = 0$ includes all y-values from 0 to 1. This property can be significant if the derivative z is treated as a probability density for which

$$(3.5)\quad \int_0^\infty z(x)\,dx = 1.$$

Note that (3.5) is false for a type 1 curve, since $z(x)$ then integrates to $1-y'$, a number less than 1.

A second feature of the curve types is summarized in Table 5. As proved in Appendix B, the slope of the curve at the intercept is either 0 or ∞ (except possibly when $b = -1$ or $c = 1$). This might seem a severe limitation on the family of curves proposed here, particularly if x'' or y' has biological significance. In practice, however, curves often have a second inflection point extremely close to the intercept. Consequently, on a reasonable scale for x, the curve $y(x)$ can appear to intercept the x- or y-axis with finite slope. Intercepts where $z = \infty$ can pose practical problems in some analyses, and we discuss these further in connection with the likelihood functions presented in Section 5.

4. Special Cases

In this section we examine the practical significance of the transform parameters b and c. We show that, if one is fixed, the other serves to define the shape of the curve between the points (x_1,y_1) and $(x_2,y_{,2})$. Thus, we refer to b and c as *shape parameters*. We show that they are somewhat redundant, and we describe rational procedures for fixing one of them.

As an aid to the discussion, we introduce the notation $\{b =$ constant$\}$ and $\{c =$ constant$\}$ to indicate families of curves with the specified values of b or c. Figure 4 represents the six such families that result from fixing b or c at -3, 0, and 3. Within each family (i.e. each panel of Fig. 4), five curves are shown, corresponding to the following values of the free parameter: -6, -3, 0, 3, and 6. The curve families were constructed by fixing the coordinates (x_1,y_1) and (x_2,y_2) at (1,0.3) and (2,0.8), respectively. The curves appear as a bundle between these two points and fan out below and above them.

Figure 4 illustrates the feature mentioned above. With one fixed parameter (b or c), the other governs the shape of the curve between the two specified points. Some curve families are more robust than others to the shape parameter. For example, the family $\{b = 3\}$ includes a broader range of shapes than the family $\{c = -3\}$. For a given application, it is advantageous to choose a family with a wide range of possible shapes. Within such a family, the shape parameter is more likely to be estimable because it significantly influences curve shape.

Figure 4 suggests that the family $\{c =$ constant$\}$ is, in general, more restrictive than the family $\{b =$ constant$\}$. This is due to the behaviour of each family as the shape parameter tends to $\pm\infty$. As indicated in Table 6 and proved in Appendix D, the three curve families $\{b = -\infty\}$, $\{c = -\infty\}$, and $\{c = +\infty\}$ each reduce to a single discontinuous curve (Fig. 5A). By contrast, the family $\{b = +\infty\}$ is still a proper family (Fig. 5B), analogous to those illustrated in Fig. 4. Equations [6.3]–[6.8] are similar to their counterparts in Table 2, except that β and η are not defined as $b \to +\infty$. In spite of this, the model still defines linkages among x, ξ, and y as $b \to +\infty$ (Appendix D).

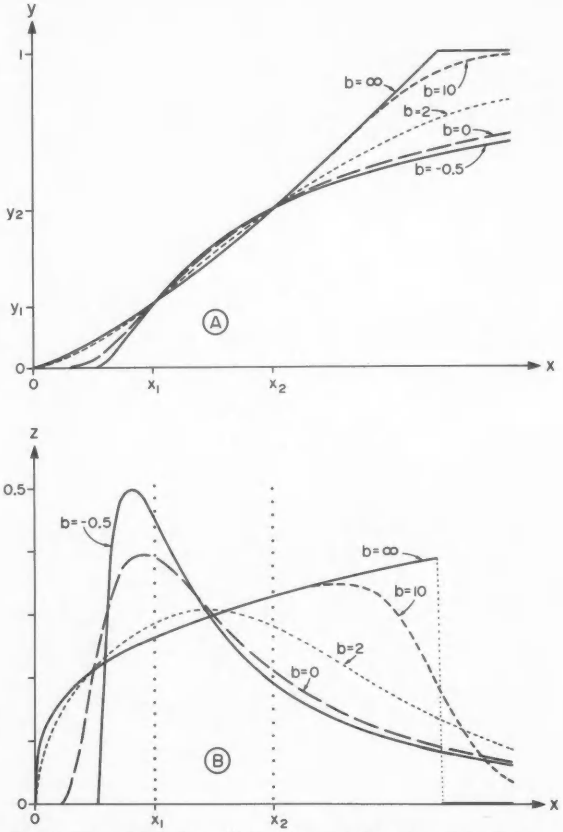

FIG. 6. Curve family $\{c = 0\}$ for (A) y and (B) z, formed by fixing $y_1 = 0.2$, $y_2 = 0.5$, and $x_2/x_1 = 2$. Each panel includes five curves corresponding to $b = -0.5$, 0, 2, 10, and ∞. All curves in Fig. 6B have 20 and 50% of their area to the left of the dotted lines at x_1 and x_2, respectively.

Figure 5A shows that the limiting curves [6.1]–[6.2] as $c \to -\infty$ and $c \to +\infty$, respectively, include the upper left and lower right boundary of the rectangle

$$(4.1)\quad R = \{(x,y)|x_1 \leqslant x \leqslant x_2, y_1 \leqslant y \leqslant y_2\}.$$

It follows that a family $\{b =$ constant$\}$ fills R, since curves within the family converge to the boundary of R as $c \to \pm\infty$. This limiting behaviour is also fairly evident in Fig. 4A–4C. By contrast, curves within a family $\{c =$ constant$\}$ do not fill R because the limit curve [6.5] lies inside R when $x_1 \leqslant x \leqslant x_2$ (Fig. 5B). This explains the apparent restrictions to the curve families portrayed in Fig. 4D–4F as $b \to +\infty$. Thus, it would appear that forestry science has made a more robust choice with the Weibull family $\{b = -1\}$ than fishery science has with the Richards family $\{c = 1\}$. This discussion, however, takes account of only some geometric aspects of these families. As illustrated in the worked examples, an appropriate choice depends on the data set.

In some contexts, the probability density $z(x)$, rather than the cumulative probability $y(x)$, is important to the analysis. As described above in connection with (3.5), the family $\{c = 0\}$ can be useful for this purpose. In particular, if $c = 0$ and

TABLE 7. Inflection point calculations for the curve families $\{b=-1\}$, $\{c=0\}$, $\{c=1\}$, and $\{b=+\infty\}$. In each case, the simpler of the two formulas for x^* or y^* is listed. In the first three families, equations are also included for calculating $H(\eta)$ and η^*. The constants β, f, g, h, η', and η'' are given by [2.1]–[2.3], [6.3], [2.13], and [2.14], respectively.

$$\{b=-1\}$$

[7.1] $H(\eta) = c\cdot[\eta-\eta'-1+(1/c)]\cdot(e^{\eta}-e^{\eta''})$

[7.2] $\eta^* = \eta'+1-(1/c)$

[7.3] $x^* = x_1\cdot[(c-1)/(\beta f)]^{1/c}$

$$\{c=0\}$$

[7.4] $H(\eta) = (\beta f+1)e^{\eta} - g(\beta f-b)$

[7.5] $\eta^* = \ln[g(\beta f-b)/(\beta f+1)]$

[7.6a] $y^* = \left[\dfrac{\beta\,(1+b)}{\beta - b\ln(x_2/x_1)}\right]^{-1/b}; \qquad b\neq 0$

[7.6b] $y^* = e^{-[1+\ln(x_2/x_1)]/\beta}; \qquad b=0$

$$\{c=1\}$$

[7.7] $H(\eta) = (\eta-\eta')\cdot(e^{\eta}-g)$

[7.8] $\eta^* = \ln(g)$

[7.9] $y^* = (1+b)^{-1/b}$

$$\{b=+\infty\}$$

[7.10] $x^* = x_1\cdot[(1-c)/h]^{1/c}$

$b>-1$, the z-curves are unimodal (type B) and integrate to 1. Figure 6 represents this family when $b = -0.5, 0, 2, 10$, and ∞. For reasons connected with a worked example in Section 5, we choose $y_1 = 0.2$, $y_2 = 0.5$, and $x_2/x_1 = 2$ in this figure. Notice that comparatively minor changes in y (Fig. 6A) correspond to major changes in z (Fig. 6B). In particular, the mode of the z-curve shifts to the right as b increases. As b tends to -1, the curve becomes discontinuous on the left; similarly, as $b \to +\infty$, a discontinuity develops on the right. All curves in Fig. 6B have 20% ($y_1 = 0.2$) of their area to the left of the dotted line at x_1, and the line at x_2 divides their area in half ($y_2 = 0.5$).

For the four families $\{b = -1\}$, $\{c = 0\}$, $\{c = 1\}$, and $\{b = +\infty\}$, it is possible to obtain analytical expressions for the coordinates of the inflection point (x^*,y^*) on the curve, when it exists. The second derivative ζ in [2.11] is defined by the function $H(\eta)$, and, as shown in Table 7, $H(\eta)$ can be factored when $b = -1$ or $c = 1$. For example, when $b = -1$, it is evident from [7.1] that $H(\eta) = 0$ when $\eta = \eta'+1-(1/c)$ or $\eta = \eta''$. By the criterion (3.4), it turns out that the relevant root of $H(\eta)$ is $\eta^* = \eta'+1-(1/c)$, as indicated in [7.2]. A similar analysis applies to the case when $c = 1$. When $c = 0$, $H(\eta)$ in [7.4] has only one root; similarly, when $b = +\infty$, it is evident from [6.7] that $\zeta(x)$ has a unique root. Table 7 shows the analytical results for each case, with the expression for x^* or y^*, whichever is simpler. Notice, in particular, that [7.3] and [7.9] provide analytical expressions for locating inflection points on Weibull and Richards curves, respectively. Furthermore, [7.9] corresponds to equation (30) in Schnute (1981), given the restriction (2.15) that $y_\infty = 1$. In making this comparison, recall that "b" here has the opposite sign of "b" in Schnute (1981).

We complete this section with two final comments on the model (2.8)–(2.11). First, it fits into the context of the general linear model (McCullagh and Nelder 1983) when both parameters b and c are presumed known prior to the analysis. When either shape parameter is considered unknown, then the model becomes nonlinear. This is not cause for serious concern, however, because (as described later) we can still use general methods to find parameter estimates and confidence regions.

Second, as indicated in the introduction, certain cases of the model are self-consistent for different measures of size. For example, suppose that the family $\{b = \text{constant}\}$ is applied to two data sets, involving length and weight data, respectively. Let c_l and c_w denote the corresponding shape parameters. Then, if weight w is exactly proportional to the cube of length l, it turns out that

$$c_l = 3c_w. \tag{4.2}$$

Thus, for instance, the square of a weight variable is equivalent to the sixth power of a length variable. A similar self-consistency applies to the family $\{c = 0\}$.

5. Likelihood and Parameter Estimation

As discussed in the Introduction, there are two fundamentally different classes of data to which model (2.8)–(2.12) applies. Bliss (1937) recognized their distinction and used the terms dose–mortality and time–mortality. Since the model has broader generality than implied by Bliss' terms, we simply refer to class A and class B data. The likelihood functions necessarily differ for these two classes and both are presented in this section.

Class A data consist of pairs (x_i,u_i), $i = 1,\ldots,n$, where x_i is a real variable in the range $(0,\infty)$ and u_i is a binary variable that takes states 0 and 1. For example, if a sample of n fish is collected from a commercial catch, then x_i could represent the size of fish i and u_i its maturity status (immature and mature). The probability $y(x_i,\Theta)$ that a fish of size x_i is mature is determined by the point binomial distribution (Mood and Graybill 1963, p. 65), where Θ represents the parameter set discussed in the previous sections. In a typical application, for example, $\Theta = (x_1,x_2,c)$. Hence, the likelihood function

$$L(\Theta) = \prod_{i=1}^{n} [y(x_i,\Theta)^{u_i}[1-y(x_i,\Theta)]^{1-u_i}] \tag{5.1}$$

is simply the product of point binomial probabilities.

In most cases, however, the analysis involves data grouped into intervals such as size ranges. To state the likelihood function for the grouped case necessitates a change in notation. Let $x_0, x_1,\ldots,x_k$ now represent the end points of a sequence of k intervals where the ith interval is (x_{i-1},x_i). Let n_i be the number of fish and m_i the number of mature fish with sizes in the ith interval. An approximate likelihood function for the grouped case is given by

$$L(\Theta) = \prod_{i=1}^{k} \left\{ y\left(\frac{x_{i-1}+x_i}{2}, \Theta\right)^{m_i} \times \left[1-y\left(\frac{x_{i-1}+x_i}{2}, \Theta\right)\right]^{n_i-m_i} \right\}. \tag{5.2}$$

Notice that (5.2) is identical to (5.1) if it is assumed that each fish in the ith interval is equal in size to the interval mean $(x_{i-1}+x_i)/2$.

Some authors (e.g. Berkson 1944, p. 360; Ashton 1972, p. 25; Welch and Foucher 1988, equation (2)) would include the product of binomial coefficients

$$P = \prod_{i=1}^{k} \frac{n_i!}{m_i!\,(n_i-m_i)!}$$

as a factor in the definition of $L(\Theta)$ for the grouped case. Technically, this is correct because the random variables are now the counts m_i, which can take integer values from 0 to n_i, rather than the two-state variables u_i. Thus, the quantities m_i are binomially distributed, in contrast with the point binomial distribution for u_i. This technicality plays no significant role in the analysis, however, because the product P is independent of the parameter vector Θ. Parameter estimates and confidence intervals are not affected when the likelihood function is multiplied by a constant.

In this discussion of class A data, notice that only the observation u_i in the data pair (x_i,u_i) is treated as a random variable. Similarly, in the grouped case, m_i is considered a random variable and n_i is not. In practice, however, the observed fish lengths x_i $(i = 1,\ldots,n)$ often come from a random sample of the catch. Thus, the lengths typically *are* random variables, with a distribution determined by the combined effects of catchability and population size structure. Even in this case, the likelihood functions (5.1)–(5.2) apply, provided that the length distribution is independent of the parameter vector Θ in the maturity model.

By contrast with class A data, class B data consist of single measurements x_i, $i = 1,\ldots,n$, real variables in the range $(0,\infty)$. For example, if n fish are monitored following their exposure to a toxicant, then the datum for fish i could be x_i, the time of death. In class A data, the value x_i is presumed known, and the random variable u_i is binary, whereas in class B data, the random variable x_i is real. The probability density function for x_i is given by the first derivative z in [2.10]. Hence, the likelihood for class B data is simply

$$(5.3)\quad L(\Theta) = \prod_{i=1}^{n} z(x_i,\Theta),$$

the product of the probability densities.

As before, the data may be grouped into k intervals (x_{i-1}, x_i) for $i = 1,\ldots,k$. In this case, let n_i be the number of deaths in the ith interval, with the total number $n = \Sigma(n_i)$. Thus, the data now consist of k integers n_i, rather than n real numbers x_i. An approximate grouped likelihood could be obtained from (5.3) by analogy with (5.1)–(5.2). This approximation is unnecessary, however, as

$$(5.4)\quad L(\Theta) = \prod_{i=1}^{k} [y(x_i,\Theta)-y(x_{i-1},\Theta)]^{n_i}$$

is the exact likelihood. In (5.4), since $y(x_i,\Theta)$ represents the cumulative probability, the difference $y(x_i,\Theta)-y(x_{i-1},\Theta)$ is the probability of occurrence within the ith interval. Thus, (5.4) is simply the multinomial likelihood associated with probabilities of occurrence in the k intervals. Technically, the multinomial coefficient $n!/\Pi(n_i!)$ should be included as a factor in the definition of $L(\Theta)$ (Mood and Graybill 1963, p. 69), but, as in the case for class A grouped data, this has no effect on the analysis.

For convenience, we obtain parameter estimates, confidence intervals, and confidence regions from twice the negative log likelihood

$$l = -2 \ln [L(\Theta)].$$

Formulas for $l(\Theta)$ corresponding to (5.1)–(5.4) are, respectively,

$$(5.5)\quad l(\Theta) = -2 \sum_{i=1}^{n} \{u_i \ln[y(x_i,\Theta)] + (1-u_i) \ln [1-y(x_i,\Theta)]\}$$

$$(5.6)\quad l(\Theta) = -2 \sum_{i=1}^{k} \left\{m_i \ln\left[y\left(\frac{x_{i-1}+x_i}{2}, \Theta\right)\right] + (n_i-m_i) \ln\left[1-y\left(\frac{x_{i-1}+x_i}{2}, \Theta\right)\right]\right\}$$

$$(5.7)\quad l(\Theta) = -2 \sum_{i=1}^{n} \ln[z(x_i,\Theta)]$$

$$(5.8)\quad l(\Theta) = -2 \sum_{i=1}^{k} n_i \ln[y(x_i,\Theta)-y(x_{i-1},\Theta)].$$

The minimum of $l(\Theta)$ determines the maximum likelihood parameter estimate $\hat{\Theta}$. In the worked examples below, we use the simplex search method (Nelder and Mead 1965; Press et al. 1986, p. 289–293), as implemented by Mittertreiner and Schnute (1985).

One technical difficulty can occur in applications to class B data. As illustrated in Fig. 3, the derivative z includes singularities (i.e. values of x at which $z = \infty$) in curve types A or C. Thus, the minimum value of l in (5.7) can theoretically be $-\infty$ if one observation x_i occurs at a singularity of z. In this case, the search for a minimum of l may not converge or may lead to anomalous results. The family $\{c = 0\}$ with $b > -1$ has properties that are particularly appropriate for class B data analysis, as suggested earlier in connection with (3.5) and Fig. 6. We illustrate these points in a worked example below.

The function $l(\Theta)$ can be used to determine confidence regions, as well as estimates, for the model parameters. To be precise, suppose that Θ has dimension r and that Θ_1 is an s-dimensional subset of Θ. Let Θ_2 denote the remaining set of r–s parameters, so that $\Theta = (\Theta_1,\Theta_2)$. To determine a confidence region for Θ_1, regarding the other parameters Θ_2 as nuisance parameters, define

$$(5.9)\quad l_1(\Theta_1) = \min_{\Theta_2} l(\Theta_1,\Theta_2).$$

Thus, given Θ_1, $l_1(\Theta_1)$ represents the minimum value of $l(\Theta)$ with respect to the nuisance parameters Θ_2. Let Θ denote the estimate of the entire parameter vector $\hat{\Theta}$ obtained by minimizing $l(\Theta)$. Then, for $0 < p < 1$, the boundary of a p-level confidence region for Θ_1 is determined by values of Θ_1 that solve the equation

$$(5.10)\quad l_1(\Theta_1) = l(\hat{\Theta}) + \chi^2(s,p),$$

where $\chi^2(s,p)$ represents the cutoff at level p for the χ^2 distribution with s df. This region is approximate, based on the likelihood ratio test for large sample sizes (Kendall and Stuart 1979, chap. 24).

Solving for p in (5.10) gives

TABLE 8. Parameter estimates for quillback rockfish length-at-maturity data (class A) and corresponding minimum values of the likelihood function $l(\Theta)$. In all cases, one or both of the parameters b and c have fixed values, indicated by an asterisk. Values of the prescribed parameters (y_1,y_2) are (0.5,0.75). Parameters x_1 and x_2 have units centimetres, while all other parameters are dimensionless.

Case	b	c	x_1	x_2	$l(\Theta)$
1	−1*	9.32	29.3	31.5	332.52
2	0*	5.11	29.1	31.2	330.69
3	1*	2.27	29.2	31.1	330.68
4	3.90	−1*	29.3	31.3	330.70
5	2.52	0*	29.3	31.2	330.83
6	1.66	1*	29.2	31.1	330.80
7	−1*	1*	27.1	32.7	418.33
8	0*	1*	28.4	31.2	347.64
9	1*	0*	28.8	31.0	334.56
10	1*	1*	29.0	31.0	331.85

$$(5.11) \quad p = (\chi^2)^{-1}[s, l_1(\Theta_1) - l(\hat{\Theta})]$$

where $(\chi^2)^{-1}$ denotes the inverse of the function $\chi^2(s,\cdot)$ in (5.10). The expression (5.11) gives an approximate p-level for rejecting a proposed value of Θ_1. A graph of p versus Θ_1 from (5.11) is called a *probability profile* for Θ_1. When $s = 1$, the profile is typically a V-shaped curve centered at $\hat{\Theta}_1$. The distance across the "V" increases as p increases, corresponding to broader confidence invervals for Θ_1 at greater levels of certainty p.

In the worked examples below, r is typically 3 and $\Theta = (x_1,x_2,c)$; s may be chosen to be 1 or 2. For example, we may wish to consider the shape parameter c without regard to the values of x_1 or x_2. In this case, $s = 1$ since the single parameter c is of interest. Alternatively, we may wish to treat c as a nuisance parameter and compute a joint confidence region for (x_1,x_2), in which case $s = 2$. Finally, if we wish to obtain a confidence interval for x_1 or x_2 alone (regarding the other two parameters as nuisance parameters), then $s = 1$.

6. Examples

6A. Class A: Quillback Rockfish (*Sebastes maliger*) Maturity

To illustrate class A data analysis, we examined the size at maturity of female quillback rockfish from a stock near Campbell River, British Columbia. During research surveys in 1986 and 1987, quillback rockfish were measured for length, weight, sex, and maturity status (Richards and Cass 1987; Richards and Hand 1987). Similar data were also collected from two samples of the commercial handline rockfish fishery in the same area during January 1986 and May 1987. For our purposes here, the four data sets were pooled without regard to possible among-sample differences. We converted the seven-point scale used for classifying maturity status (adapted from Westrheim 1975) to a binary scale to represent immature (0) or mature (1) fish. Fish were grouped into 5-mm size intervals for length and 20-g size intervals for weight.

Parameter estimates for quillback rockfish length-at-maturity were obtained from (5.6) following the methods described in the previous section. To illustrate the effect of the shape parameter, Table 8 lists parameter estimates for curve families with b or c fixed at −1, 0, or 1, as well as the special cases in Table 1 with both shape parameters fixed. The lowest value of $l(\Theta)$ in Table 8 (case 3) is obtained in the family $\{b = 1\}$, i.e. the logit–exponential model. The resulting curve for this case is illustrated in Fig. 7. The figure also includes probability profiles for x_1 and x_2 obtained from (5.11). Approximate 95% confidence intervals for x_1 and x_2, namely

$$(6.1) \quad 28.5 < x_1 < 29.8, \qquad 30.5 < x_2 < 31.8,$$

are determined by the x-coordinates at the intersections of the profiles with the line $p = 0.95$.

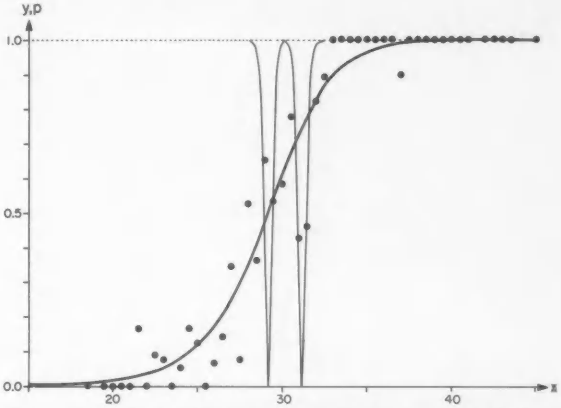

FIG. 7. Data points (circles), y-curve (solid line), and probability profiles for x_1 and x_2 (thin lines) for quillback rockfish length-at-maturity data (class A). Parameter values correspond to case 1 in Table 8.

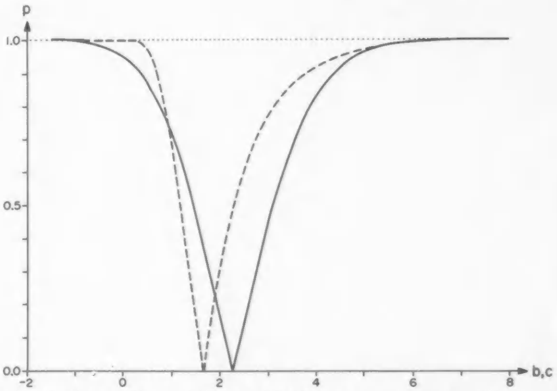

FIG. 8. Probability profiles for b with fixed $c = 1$ (broken line) and c with fixed $b = 1$ (solid line) for quillback rockfish length-at-maturity data (class A) with $y_1 = 0.5$ and $y_2 = 0.75$.

It is apparent from Table 8 that there is little distinction in the likelihood function or parameter estimates among cases 1–6 for which either b or c is allowed to be free. Similarly, the classical logistic model (case 10) appears to be appropriate for these data. In contrast, however, the von Bertalanffy (case 7), Gompertz (case 8), and logit–log (case 9) models result in much higher values of $l(\Theta)$. Based on (5.11), the hypothesis of a fixed c for cases 7, 8, and 9 can be rejected at the 95% confidence level in favour of the corresponding case with c free (cases 1, 2, and 3, respectively). This is also illustrated by the probability profiles for b and c in Fig. 8. For fixed $b = 1$, the 95% confidence interval for c is (0.01,4.79). Similarly, for fixed $c = 1$, the 95% confidence interval for b is (0.59,4.48).

Cases 7–9 in Table 8 illustrate the potential limitations of a two-parameter model in which both b and c are arbitrarily fixed.

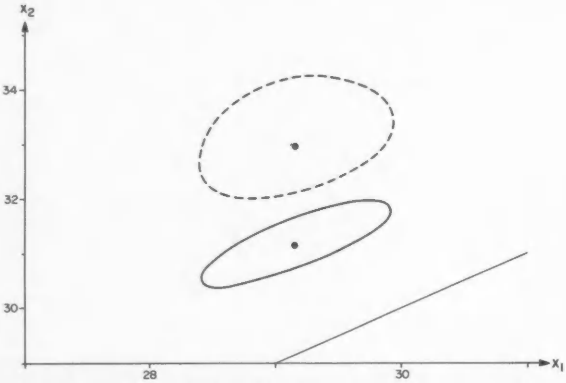

FIG. 9. Approximate 95% confidence regions for (x_1, x_2), based on quillback rockfish length-at-maturity data (class B) with $b = 1$, $y_1 = 0.5$, and either $y_2 = 0.75$ (solid line) or $y_2 = 0.9$ (broken line). Circles at the region centers indicate point estimates. For reference, the line $x_1 = x_2$ is also shown.

The choices of fixed parameters in cases 7 and 8 are particularly inappropriate for the maturity data. Conversely, given the redundancies among curve families portrayed in Fig. 4 and the similarities among cases 1–6 in Table 8, it is evident that four parameters are too many. Our approach is to treat the choice of family $\{b = \text{constant}\}$ or $\{c = \text{constant}\}$ somewhat informally, as in the choice $\{b = 1\}$ here. We then treat the resulting three-parameter model formally in obtaining estimates and confidence intervals. This means, for example, that the intervals (6.1) take account of the uncertainty in the third parameter c. It is true, of course, that certain fixed values of b and c may appear to represent the data adequately, as in case 10 of Table 8. Confidence intervals based on such a two-parameter model may, however, be unrealistically narrow because they fail to account for uncertainties inherent in another unknown parameter.

As discussed in connection with (4.2), one feature of our model is that for certain cases, it is self-consistent for different measures of size. We are able to test this self-consistency for the rockfish data, as both length and weight were measured. For example, with b fixed at 1, we obtain the estimates $\hat{c}_l = 2.27$ and $\hat{c}_w = 0.57$. The ratio $\hat{c}_l / \hat{c}_w = 3.98$ can be compared with the predicted ratio of 3 from (4.2). When the uncertainties in $\hat{c}_l$ and $\hat{c}_w$ are taken into account, a ratio of 3 cannot be rejected.

One aspect of the model that we have so far not discussed in detail is the appropriate choice for (y_1,y_2). The importance of this choice is illustrated by 95% confidence regions for (x_1,x_2) in Fig. 9. There are two regions in Fig. 9, obtained by choosing (y_1,y_2) to be either (0.5,0.75) or (0.5,0.9). Since y_1 is the same in each case, both regions have the same width horizontally and thus indicate the same uncertainty in x_1. (This occurs because the minimum value of $l(\Theta)$ is independent of the choice y_2.) By contrast, the upper region in Fig. 9 is broader vertically than the lower region, indicating greater uncertainty in x_2 when $y_2 = 0.9$. This difference can be understood by examining Fig. 7. The data points lie closer to the predicted curve in the region $y = 0.75$ than in the region $y = 0.9$, that is, the curve is better determined near $y = 0.75$. Incidentally, convergence in parameter estimation will occur more rapidly if the fixed values (y_1,y_2) are chosen in a region where the curve is well determined.

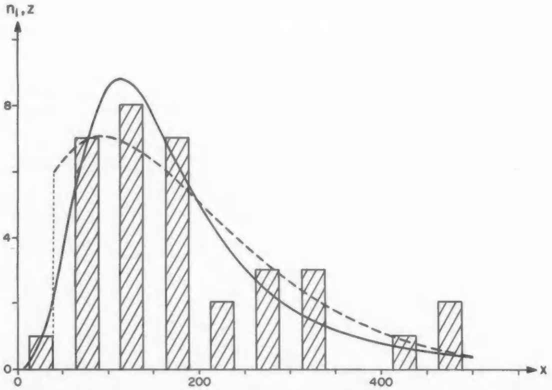

FIG. 10. Frequency histogram for speckled trout fry time–mortality data (class B) grouped by 50-min intervals, along with the density curves $z(x)$ corresponding to case 1 (broken line) and case 2 (solid line) in Table 9. Values of z have been scaled by the factor $50 \cdot n$ ($n = 34$) to conform to the scale of the histogram.

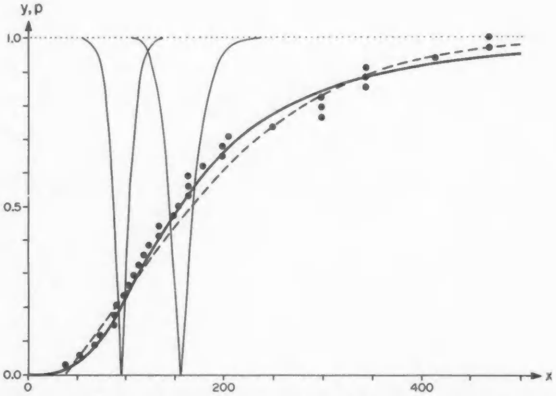

FIG. 11. Data points (circles), y-curve (solid line), and probability profiles for x_1 and x_2 (thin lines) for speckled trout fry time–mortality data (class B), with parameter values corresponding to case 2 in Table 9. The broken line represents the y-curve corresponding to case 1 in Table 9.

6B. Class B: Speckled Trout (*Salvelinus fontinalis*) Mortality

To illustrate the analysis of class B data, we use the data of Shepard (1955, p. 436) for the mortality times of speckled trout fry exposed to an oxygen concentration of 1.25 mg/L. Shepard (1955) stated that observations "were carried out more or less continuously," and so we assume the data to be ungrouped. For comparison, however, we also present analyses for data grouped by 5- and 50-min time intervals.

Class B data are typically displayed as either a density histogram or a cumulative scatter plot. We illustrate both approaches in Fig. 10 and 11. Note that most of the deaths occurred near the beginning of the time series, with widely spaced and multiple deaths near the end of the series. This is apparent from the skew of the histogram in Fig. 10 and from the location of the data points in Fig. 11. Hence, x_1 and x_2 are better determined for choices of y_1 and y_2 on the lower part of the y-curve in Fig. 11, and we chose $y_1 = 0.2$ and $y_2 = 0.5$ accordingly. This contrasts with the class A data example,

TABLE 9. Parameter estimates for speckled trout fry time–mortality (class B) data and corresponding minimum values of the likelihood function $l(\Theta)$. The analysis is based either on ungrouped data ($\Delta x = 0$) or on grouped data with interval width $\Delta x > 0$. In all cases, one or both of the parameters b and c have fixed values, indicated by an asterisk. Values of the prescribed parameters, $(y_1 y_2)$ are (0.2,0.5). Parameters x_1 and x_2, along with the interval width Δx, have units minutes, while all other parameters are dimensionless.

Case	Δx	b	c	x_1	x_2	$l(\Theta)$
1	0	−1*	1.49	88.5	165.4	407.08
2	0	0.76	0*	94.8	155.4	410.37
3	0	1*	0*	94.8	157.6	410.50
4	5	1.01	0*	94.3	158.2	298.67
5	5	1*	0*	94.3	158.0	298.67
6	50	0.95	0*	96.2	157.2	143.94
7	50	1*	0*	96.2	157.6	143.95

where more information on maturity was available for larger fish. Note that the choices of y_1 and y_2 here match those in Fig. 6 above, where we indicated that the family $\{c = 0\}$ portrayed in Fig. 6B might be appropriate for class B data.

Table 9 lists parameter estimates obtained by minimizing the likelihood functions (5.7) for ungrouped data and (5.8) for grouped data. There are seven cases in the table. Case 1 is included to illustrate some of the problems associated with discontinuities in z. Cases 2–7 illustrate the curve family $\{c = 0\}$ with either b free or $b = 1$ (logit–log), for ungrouped and grouped data. With the exception of case 1, estimates of x_1 and x_2 are similar for the different cases. There are only minor increases in $l(\Theta)$ associated with fixed $b = 1$ compared with b free. In fact, Shepard (1955) used a probit–log analysis for these data, which is comparable with our logit–log analysis in case 3. Furthermore, the choice of grouping interval altered the estimates of x_1 and x_2 by at most 2 min.

Although the value of $l(\Theta)$ in Table 9 for case 1 is lower than the value for corresponding cases 2 and 3, we recommend case 2 as the best for this data set. The reason for this choice can be understood by examining the density curves for cases 1 and 2 in Fig. 10. The curve for case 2 is a smooth curve that passes reasonably through the data. In contrast, the case 1 curve is discontinuous and drops to 0 for a value of x'' slightly less than the x-value of the first data point (37 min). Instabilities in the analysis can result from x'' being assigned a value greater than the first x-value during the minimization process. Differences between cases 1 and 2 are less pronounced in the y-curves (Fig. 11). Case 1 appears to be a slightly better fit in the lower and upper regions of the curve, and case 2 appears to be better in the middle region. Note that the case 1 curve contacts the x-axis with a finite slope, a general feature of the curve family $\{b = -1\}$.

Probability profiles for x_1 and x_2 are also shown in Fig. 11 for the case 2 example. The profile for x_1 is somewhat narrower than for x_2, indicating that x_1 is better determined. The reason for this is apparent in examining the data points. The time interval between observations is less in the region near x_1 than near x_2.

In summary, it appears that class A data are relatively robust to the choice of curve family. This is less true for class B data, due to discontinuities in the topology of the density curve families, although the family $\{c = 0\}$ appears to have fairly broad utility. In general, the model (2.8)–(2.12), together with the likelihood functions (5.5)–(5.8), gives perspective to a wide range of historical techniques. Practically, the model's flexible choice of parameters allows the investigator to focus on quantities of greatest interest, such as size at 50% maturity or time to 50% mortality. We find that the model provides a useful analytic tool, both for application to a particular data set and for assessing the results in the light of classical theory.

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Appendix A. Model Equations

This appendix gives proofs of the model equations in Table 2. We defer proofs of the cases $b = 0$ and $c = 0$ to the end. Note that only equations [2.4]–[2.11] require proof, since the remaining equations are definitions, where the definition of β in [2.1] agrees with (2.10). Furthermore, [2.4]–[2.6] are straightforward algebraic consequences of (2.11), (2.8), and (2.9), respectively, and [2.7]–[2.9] are simply the inverses of [2.4]–[2.6]. Thus, it remains only to prove the expressions [2.10]–[2.11] for the derivatives z and ζ.

To do so, note from [2.4] that

$$\text{(A.1)} \quad d\xi/dx = (f/x_1)\cdot(x/x_1)^{c-1}.$$

Similarly, since

$$\text{(A.2)} \quad y^{-b} = 1 + bge^{-\eta},$$

from [2.6], it follows that

$$\text{(A.3)} \quad dy/d\eta = gy^{b+1}e^{-\eta}.$$

By the chain rule

$$\frac{dy}{dx} = \frac{dy}{d\eta} \cdot \frac{d\eta}{d\xi} \cdot \frac{d\xi}{dx},$$

it follows from (A.1) and (A.3) that

$$\text{(A.4)} \quad z = [gy^{b+1}e^{-\eta}]\cdot\beta\cdot[(f/x_1)\cdot(x/x_1)^{c-1}],$$

since $d\eta/d\xi = \beta$ from [2.5]. This proves [2.10], since, from (A.2),

$$\text{(A.5)} \quad gy^be^{-\eta} = (1-y^b)/b.$$

To derive [2.11], write [2.10] in the form

$$\text{(A.6)} \quad z = \delta x^{c-1}(y-y^{b+1})$$

where

$$\text{(A.7)} \quad \delta = (\beta f)/(bx_1{}^c).$$

Differentiating (A.6) as a product of function of x and y gives

$$\text{(A.8)} \quad dz/dx = (c-1)\delta x^{c-2}(y-y^{b+1}) \\ + \delta x^{c-1}[1-(b+1)y^b]z,$$

since $dy/dx = z$. Using (A.6), one can rewrite (A.8) in the form

$$\zeta = (z/x)\cdot[\delta x^c(1-y^b-by^b) + (c-1)] \\ = (y^bz/x)\cdot[\delta x^c(y^{-b}-1-b) + (c-1)y^{-b}].$$

Taking account of (A.2), this proves that

$$\text{(A.9)} \quad \zeta = -(y^bz/x)\cdot[\delta x^c(b-bge^{-\eta}) + (1-c)(1+bge^{-\eta})].$$

Furthermore, from [2.7] and (A.7), it follows that

$$\delta x^c = (\beta f/b) + (c/b)\cdot(\beta\xi),$$

that is, from [2.5]

$$\text{(A.10)} \quad \delta x^c = (1/b)\cdot(\beta f + c\eta).$$

Combining (A.9) and (A.10) gives the expression [2.11] for ζ.

The results when $b = 0$ or $c = 0$ in Table 2 are all straightforward consequences of the limit formulas

$$\text{(A.11)} \quad \lim_{u\to 0} \, (v^u-1)/u = \ln(v)$$

$$\text{(A.12)} \quad \lim_{u\to 0} \, (1+uv)^{1/u} = e^v.$$

In [2.10b], note that, when $b = 0$,

$$-\ln(y) = -\ln(y_1)\cdot e^{-\eta} = ge^{-\eta}$$

from [2.6b] and [2.3b]. This completes the proof of Table 2.

Appendix B. Curve Types

The model's four curve types result from interrelated ranges of x, ξ, η, and y. For example, if $c > 0$ in the relationship [2.4] between x and ξ, it follows that $\xi(0) = -f/c$ and $\xi(\infty) = \infty$. Since $\xi' = \eta'/\beta = -f/c$ from [2.13], it follows that ξ goes from ξ' to ∞ when x goes from 0 to ∞. More generally, one can show that the first range implies the second range in the following table:

Condition	1st range	2nd range
$c > 0$	$x: 0 \to \infty$	$\xi: \xi' \to \infty$
$c < 0$	$x: 0 \to \infty$	$\xi: -\infty \to \xi'$
$b > 0$	$\eta: -\infty \to \infty$	$y: 0 \to 1$
$b < 0$	$\eta: \eta'' \to \infty$	$y: 0 \to 1$

The last two lines in this table follow from [2.6], taking account of [2.14] when $b < 0$. For example,

$$y = [1 - e^{\eta''-\eta}]^{-1/b}$$

when $b < 0$.

The table above leads logically to the ranges shown in Table 3 for the four curve types. For example, if $b > 0$ and $c > 0$, the model implies the following sequence of ranges:

(B.1) $x{:}0 \rightarrow \infty,\ \xi{:}\xi' \rightarrow \infty,\ \eta{:}\eta' \rightarrow \infty,\ y{:}y' \rightarrow 1,$

as in the first line of Table 3. Thus, for positive values of x, the lowest value of y is y', with $0 < y' < 1$. If $b < 0$ and $c > 0$, there are two possibilities, namely,

(B.2a) Type 1: $\eta' > \eta''$

(B.2b) Type 2: $\eta'' > \eta'$.

In the case (B.2a), the variable ranges are those shown in (B.1). In (B.2b), however, the value $x = 0$ corresponds to η', a value lower than η''. From the table above, when $b < 0$, η'' is the lowest possible η-value corresponding to a y-value in the range (0,1). Consequently, y must be defined 0 when $0 \leqslant x \leqslant x''$ (as it is by the definitions in Appendix C), and the ranges

(B.3) $x{:}x'' \rightarrow \infty,\ \xi{:}\xi'' \rightarrow \infty,\ \eta{:}\eta'' \rightarrow \infty,\ y{:}0 \rightarrow 1$

agree with those shown in Table 3 for curves of type 2. Similar logic determines the ranges for types 3 and 4 when $c < 0$. In particular, notice from [2.13]–[2.14] that $\eta' > 0 > \eta''$ when $b < 0$ and $c < 0$, since $-bg = 1 - y_1^{-b} < 1$ when $b < 0$.

By (B.2), the boundary in the second quadrant between curves of types 1 or 2 is determined by the condition $\eta' = \eta''$, i.e. from [2.1]–[2.3] and [2.13]–[2.14]:

$$\text{(B.4)}\quad -\ln\left[\frac{1-y_1^{-b}}{1-y_2^{-b}}\right] \cdot \frac{x_1^c}{x_2^c - x_1^c} = \ln(1-y_1^{-b}).$$

Solving for c in (B.4) gives

$$\text{(B.5)}\quad c = \frac{\ln\left[\dfrac{\ln(1-y_2^{-b})}{\ln(1-y_1^{-b})}\right]}{\ln(x_2/x_1)}.$$

This proves that the second quadrant boundary between types 1 and 2 is given by the curve $\gamma(b)$ in (3.3).

Our proof so far has established the variable ranges listed in Table 3 and illustrated in Fig. 2. We must now account for the subtypes A, B, and C associated with zero, one, or two inflection points, respectively. Notice from [2.11]–[2.12] that an inflection point can occur only at a value of η where $H(\eta) = 0$. A short calculation shows that the first and second derivatives $H_1(\eta) = dH/d\eta$ and $H_2(\eta) = d^2H/d\eta^2$ are, respectively,

(B.6) $H_1(\eta) = (c\eta + \beta f + 1)e^{\eta} - cg$

(B.7) $H_2(\eta) = (c\eta + \beta f + 1 + c)e^{\eta}$.

For each of the functions H, H_1, and H_2, the dominant term as $\eta \rightarrow -\infty$ or $\eta \rightarrow +\infty$ is listed below:

η	$H(\eta)$	$H_1(\eta)$	$H_2(\eta)$
$-\infty$	$-cg\eta$	$-cg$	$c\eta e^{\eta}$
$+\infty$	$c\eta e^{\eta}$	$c\eta e^{\eta}$	$c\eta e^{\eta}$

Since $g > 0$, these dominant terms can be used to infer the signs of H, H_1, and H_2 as $\eta \rightarrow \pm\infty$. Thus, for large negative values of η, it follows from the above table that $H(\eta)$ has the same sign as c. Similarly, one can obtain the signs listed below, based on η and the sign of c:

η	c	$H(\eta)$	$H_1(\eta)$	$H_2(\eta)$
$-\infty$	+	+	−	−
$+\infty$	+	+	+	+
$-\infty$	−	−	+	+
$+\infty$	−	−	−	−

From (B.7) it follows that $H_2(\eta)$ has the unique root $\eta = -(\beta f + 1 + c)/c$. This means that $H_1(\eta)$ has exactly one critical point. Furthermore, since $H_1(\eta)$ has opposite signs as $\eta \rightarrow -\infty$ and $\eta \rightarrow \infty$, it follows that $H_1(\eta)$ has exactly one root. (The number of roots must be odd, and if there were three or more, then Rolle's theorem would prove the existence of at least two critical points.) This conclusion implies, in turn, that $H(\eta)$ has exactly one critical point. Since $H(\eta)$ has the same sign as $\eta \rightarrow -\infty$ or $\eta \rightarrow \infty$, it follows that $H(\eta)$ has at most two roots. (Again, if there were three or more, then there would be at least two critical points.) This means that the curve $y(x)$ can have at most two inflection points.

The next step in our reasoning is connected with Table 5, which shows the slope of the curve at the axis intercept for each curve type. These results come from the expression [2.10] for z. In type 1, where the intercept is $(0,y')$ with $y' > 0$, it follows from [2.10] that $z = O(x^{c-1})$ for small x. Consequently, $z \rightarrow 0$ or $z \rightarrow \infty$ when $c > 1$ or $c < 1$, respectively, as shown in the first two lines of Table 5. Similarly, in types 2 and 3, where the intercept is $(x'',0)$ with $x'' > 0$, $z = O[y - y^{b+1})/b]$ for small y. Consequently, $z \rightarrow 0$ when $b > -1$ and $z \rightarrow \infty$ when $b < -1$, as in Table 5.

Type 4 is somewhat different than types 1–3 because in this case, both x and y tend to 0 at the intercept. Let z_0 denote the slope z at (0,0), and suppose that $z_0 > 0$. Then $y \simeq z_0 x$ for x near 0. When $b > 0$ and $c < 0$ (type 4), it follows from [2.10] that $z = O(x^{c-1} \cdot x) = O(x^c)$; thus, $z \rightarrow \infty$ as $x \rightarrow 0$. This shows that the slope z_0 at (0,0), if nonzero, is ∞; consequently, z_0 must be either 0 or ∞. We show below why it must be 0, as indicated in Table 5.

The slope at the intercept is related to the number of inflection points. To see this, note that, since it is asymptotic, the curve must be convex down as $x \rightarrow \infty$. Similarly, at the intercept, the curve must be convex up when $z = 0$ and convex down when $z = \infty$. Since there can be at most two inflection points, a curve starting with $z = 0$ must have exactly one inflection point to accommodate the change in convexity. Similarly, a curve starting with $z = \infty$ must have either zero or two inflection points, corresponding, respectively, to no change in convexity or a double reversal of convexity. Thus, Table 5 shows why type 1 has subtype B when $c > 1$ and subtype A or C when $c < 1$, as indicated in Fig. 1. Similarly, the line $b = -1$ separates type 2B from types 2A and 2C. In each case, if there are two inflection points, the upper one is closest to the asymptote; this explains the definition (3.4) for η^* when $c > 0$.

Unlike types 1 and 2, it turns out that types 3 and 4 can have at most one inflection point. To see this, notice that η is bounded above by η' in types 3 and 4 and that, by [2.12], [2.13], and [2.3],

(B.8) $H(\eta') = (1-c)(e^{\eta'} - 1 + y_1^{-b})$.

Since $\eta' > 0$ and $e^{\eta'} > 1$ when $c < 0$ by [2.13], it follows that $H(\eta') > 0$ in types 3 and 4. Also, as observed earlier, $H(\eta) < 0$ as $\eta \rightarrow \pm\infty$ when $c < 0$. Thus, $H(\eta)$ has two roots when $c < 0$, but the upper root is beyond the upper limit η' for η. This shows that types 3 and 4 can have at most one inflection point, and it also accounts for the definition (3.4) of η^* when $c < 0$.

The proofs about curve types are now completed by noting from Table 5 that types 3A and 3C are theoretically possible when $b < -1$; however, since there can be at most one inflection point, type 3C is eliminated. Furthermore, in type 4, since $H(-\infty) < 0$ and $H(\eta') > 0$, it follows that there is precisely one inflection point so that only type 4B is possible. This also explains why the slope at (0,0) must be 0, but not ∞, in the last line of Table 5.

Appendix C. Computational Details

From a computational point of view, the model equations in Table 2 are not quite complete. Formulas there frequently involve the use of a power function u^v. If u is negative, then u^v is not real. Furthermore, if u is positive and v is large, then an attempt to calculate u^v may result in computer overflow or underflow.

These problems can be avoided by implementing the power function u^v as follows. First, define a bounding function

$$\text{(C.1)} \quad B(x) = \begin{cases} -C; & x < -C \\ x; & -C \leqslant x \leqslant C \\ C; & x > C \end{cases}$$

with a suitable bounding constant $C > 0$, and then let

$$\text{(C.2)} \quad u^v = \begin{cases} e^{B[v \cdot \ln(u)]}; & u > 0 \\ 0; & u \leqslant 0. \end{cases}$$

The choice of C in (3.3a) depends on the computer precision available for computing $e^{\pm C}$ without overflow or underflow. We recommend $C = 100$ or larger, if possible.

The use of (C.1)–(C.2) not only eliminates computer error, but also assures that the function *y(x)* computed from Table 2 is properly truncated in the interval [0,1], provided that the constraints (2.12) hold. In particular, the assumption (C.2) is implicit in Table 2, where we avoid more complex equations that specifically identify such truncations.

Appendix D. Infinite Shape Parameters

This appendix gives proofs of the equations in Table 4 for the families $\{b = \pm\infty\}$ and $\{c = \pm\infty\}$. It follows readily from (2.11) that

$$\text{(D.1)} \quad \lim_{c \to -\infty} \xi(x) = \begin{cases} -\infty; & 0 < x < x_1 \\ 0; & x = x_1 \\ 1; & x > x_1 \end{cases}$$

$$\text{(D.2)} \quad \lim_{c \to \infty} \xi(x) = \begin{cases} 0; & 0 < x < x_2 \\ 1; & x = x_2 \\ \infty; & x > x_2. \end{cases}$$

Since, in general, y takes the values 0, y_1, y_2, and 1 when ξ is $-\infty$, 0, 1, and ∞, respectively, the results [6.1]–[6.2] for the families $\{c = \pm\infty\}$ follow at once from (D.1)–(D.2).

Results for the families $\{b = \pm\infty\}$ can be derived from the following versions of $y(\xi)$ obtained from (2.8), (2.10), and (2.14):

$$\text{(D.3)} \quad y(\xi) = [1 - (1-y_1^{-b})^{1-\xi}(1-y_2^{-b})^{\xi}]^{-1/b}; \qquad b < 0$$

$$\text{(D.4)} \quad y(\xi) = [1 + (y_1^{-b}-1)^{1-\xi}(y_2^{-b}-1)^{\xi}]^{-1/b}; \qquad b > 0.$$

If b is large negative, then the quantities y_i^{-b} $(i = 1,2)$ in (D.3) are small; indeed, it follows that

$$\text{(D.5)} \quad y(\xi) \simeq \min\{[(1-\xi)y_1^{-b} + \xi y_2^{-b}]^{-1/b}, 1\}; \; b \simeq -\infty.$$

Similarly, if b is large positive, the quantities y_i^{-b} $(i = 1,2)$ in (D.4) are large, and

$$\text{(D.6)} \quad y(\xi) \simeq \min\{y_1^{1-\xi}y_2^{\xi}, 1\}; \quad b \simeq +\infty.$$

The upper bound of 1 in (D.5)–(D.6) reflects the fact that the exact expressions (D.3)–(D.4) have this upper bound.

Taking account of (C.1)–(C.2), it can be shown from (D.5) that

$$\text{(D.7)} \quad \lim_{b \to -\infty} y(\xi) = \begin{cases} 0; & \xi < 0 \\ y_1; & \xi = 0 \\ y_2; & \xi > 0. \end{cases}$$

Since $x = x_1$ when $\xi = 0$, this proves [6.1] for the family $\{b = -\infty\}$. Similarly, (D.6) implies [6.5], where the critical value ξ_m in [6.4] is determined by the condition $y(\xi_m) = 1$. The derivatives z and ζ in [6.6]–[6.7] are straightforward consequences of [6.5]. Finally, $\xi' = \eta'/\beta = -f/c$ by [2.14], and this proves [6.8].

Diet Selection and the Contribution of Detritus to the Diet of the Juvenile White Sucker (*Catostomus commersoni*)

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The ash-free dry mass (AFDM) of detritus, invertebrates, and algae in the diet of juvenile white sucker (*Catostomus commersoni*) was determined by quantitative microscopy. Fish were collected from a northern Michigan pond from January through October 1986 and their seasonal diet was compared with benthc invertebrate abundance. The quantity of detritus in sucker foreguts was inversely related to benthic microcrustacean densities. In July, microcrustacean densities were high and they comprised 95% of the AFDM in foregut contents. By October, microcrustacean densities had declined to 13% of their maximum density and detritus comprised over 90% of the sucker's diet AFDM. In laboratory aquaria, sucker that were fed detritus mixed with four different densities of *Artemia* ingested significantly more detritus from diets that provided lower *Artemia* densities. In the presence of high *Artemia* densities, sucker completely rejected detritus and ingested only *Artemia*. The fact that juvenile sucker can separate detritus from invertebrates that they swallow demonstrates that detritus is not ingested incidentally. Both laboratory and field data support the hypothesis that detritus is ingested intentionally when preferred invertebrate prey are scarce.

La masse sèche sans cendre (AFDM) de détritus, le nombre d'invertébrés et le volume d'algues qui composent le régime alimentaire du jeune Meunier noir (*Catostomus commersoni*) ont été déterminés par microscopie quantitative. Les poissons ont été capturés dans un étang du nord du Michigan entre janvier et octobre 1986 et l'abondance de leur régime saisonnier en invertébrés benthiques a été comparée. La quantité de détritus trouvés dans les voies intestinales antérieures du Meunier était inversement reliée à la densité des microcrustacés benthiques. En juillet, la densité de ces microcrustacés était élevée et ceux-ci constituaient 95 % de la AFDM des contenus gastriques. En octobre, la densité des microcrustacés avait baissé à 13 % du maximum et les détritus formaient plus de 90 % de la AFDM du régime des poissons. Dans les aquariums de laboratoire, les Meuniers nourris de détritus mélangés à quatre densités différentes de *Artemia* ingéraient considérablement plus de détritus avec un régime à plus faible densité de *Artemia*. En présence de fortes densités de *Artemia* les Meuniers rejetaient complètement les détritus et n'ingéraient que *Artemia*. Le fait que les jeunes Meuniers peuvent séparer les détritus des invertébrés qu'ils avalent démontre que les détritus ne sont pas ingérés par hasard. Les données de laboratoire et les données de terrain viennent appuyer toutes deux l'hypothèse que les détritus sont ingérés intentionnellement lorsque les proies invertébrées préférées sont rares.

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The white sucker (*Catostomus commersoni*) is one of the most widely distributed fishes in North America and can dominate fish community biomass (Keast 1966; Trippel and Harvey 1986). Despite observations that white sucker ingest amorphous detritus along with other identifiable plant and animal foods, the white sucker is generally considered to be a secondary consumer that feeds on benthic invertebrates and microcrustaceans (Eder and Carlson 1977; Lalancette 1977; Barton 1980). This apparent failure to consider detritus a potential food is not unique to studies of the white sucker. Many other presumed secondary consumer fish are known to ingest variable quantities of detritus, especially catostomids and cyprinids (Forbes 1888; Keast 1966; McNeely 1987).

Early views that detritus is indigestable, nutritionally insignificant to fish (Darnell 1967; Odum 1970) and ingested indiscriminately with invertebrates (Forbes 1888; Carl 1936; Macphee 1960) contributed to neglect of detritus as a food item. However, certain types of detritus have been shown to be 60–75% digested and assimilated by obligate detritivores and to be nutritionally adequate to support their growth (Bowen 1981; Lewis and Peters 1984). The role of detritus in the diet of omnivorous fish like the white sucker is poorly understood and needs to be assessed.

In this study I measured the ash-free dry mass (AFDM) of detritus, invertebrates, and algae present in the gut contents of juvenile white sucker throughout an annual cycle to assess whether enough detritus is present in the gut contents to be considered a potential food resource. I also examined the hypothesis that sucker ingest detritus intentionally and that the amount of detritus ingested varies inversely with the abundance of invertebrate prey.

Study Site

A 0.10-ha farm pond located in Houghton Co., MI (47°09′N, 88°40′W) served as the study site and source of fish and detritus for laboratory experiments. The pond is located at the edge of an old hay field and drains into an alder (*Alnus* sp.) marsh through tiles in an earthen dam constructed in 1971. The northeast shoreline is sheltered by a dense spruce (*Picea* sp.) grove. Groundwater discharges through a series of springs along the bottom and a small (<0.5 m^3/s low flow) permanent inlet stream that drains the field. This continuous flow prevents anoxic conditions and catastrophic fish mortality during periods of ice cover and during late summer when dense beds of *Potamogeton* sp. fill the water column. Substrate throughout the pond is sand and fine silt. Water temperatures from June through August range from 19 to 25°C throughout the water column. Four species of fish are abundant and reproduce in the pond or inlet stream: white sucker, golden shiner (*Notemigonus crysoleucas*), brook trout (*Salvelinus fontinalis*), and creek chub (*Semotilus atromaculatus*).

Materials and Methods

Fish Collection

Juvenile fish (35–70 mm standard length) were collected by seining at 3- to 4-wk intervals from May through October when the pond began to freeze and with minnow traps set under the ice in January and February. White sucker spawn in May. A length freqency distribution plotted from all fish captured in early May indicated that this size class represented the 1+ age class from May through June and 0+ fish from July through February. Hazardous ice conditions and low capture rates made sampling unsuccessful during other months. Fish were killed and iced immediately. The standard length of each fish was recorded and the entire gut was preserved in 10% formalin within 45 min. Only fish with full foreguts were analyzed. To assess diurnal variation in diet composition, a preliminary series of gut samples were collected over a 24-h period beginning at 0900 on July 30, 1982. Samples were collected at 2-h intervals from 1800 to 2400 and at 3-h intervals from 0000 to 1800.

Gut Content Analysis

Contents were removed from the anterior one fifth of the gut tract, up to the first bend, which delimits a recognizable foregut in this stomachless fish (Stewart 1926). To quantify invertebrates, foregut contents were agitated in 1 mL of distilled water in a test tube on a vortex mixer, diluted so that a 1-mL subsample contained 50–100 organisms (5–10 mL total volume), and suspended in a beaker with a magnetic stir bar. A 1-mL subsample was removed with a pipet and placed in a Sedgwick–Rafter counting cell (S-R cell). The entire S-R cell was scanned through a light microscope at 25×. A drawing tube calibrated against a stage micrometer was used to trace invertebrate outlines to scale on paper. The 1-mm depth of the S-R cell preserved the three-dimensional shape of food particles. In the case of foreguts containing fewer than 50 invertebrates, all foregut material was placed in the S-R cell.

The number of detritus particles in foregut contents greatly exceeds the number of invertebrates. Consequently, to quantify detritus, the first subsample was rinsed from the S-R cell back into the sample beaker and the entire sample was further diluted to 100–300 mL total volume with distilled water. A second 1-mL subsample was transferred to the S-R cell. Four or five transects, each comprising 5% of the S-R cell area, were scanned at 160× (phase contrast) until 50–100 detritus particles were counted and their outlines traced. Algae were similarly traced. Items recognized as inorganic matter, i.e. sand, were excluded from the analysis.

A single count of 50–100 items is an adequate sample of foregut contents, since the precision and accuracy associated with a single count can be estimated for randomly distributed particles that follow a Poisson distribution. Counts of 50–100 vary no more than 20–25% of the true value at the 95% significance level (Lund et al. 1958). Accuracy depends entirely on the size of the count and varies indirectly with the square root of the number counted (Lund et al. 1958). Consequently, counts 2–3 times greater than 100 do little to increase accuracy, but counts below 50 are subject to significantly greater statistical error. Analysis of counts of detritus particles and algae present in 1-mL subsamples of diluted gut contents indicated that particles were randomly distributed throughout both the sample beaker and the S-R cell (chi-square test for randomness, $p<0.05$; Lund et al. 1958).

Volumes of detritus, invertebrates, and algae were determined by measuring the length and width of each particle and calculating the volume of a similarly shaped geometric solid. Length was defined as the longest axis, and width was measured perpendicular to particle length at its midpoint. Preliminary measurements taken with a calibrated fine-focus adjustment on a light microscope confirmed that particle width closely approximated vertical height for detritus from a variety of sources. Detritus particles and diatoms shaped similarly to *Navicula* sp. were considered prolate spheroids, which slightly overestimated diatom volume. Diatoms were a small part of the diet, however, and overestimates were not expected to affect overall conclusions. Chironomid larvae and copepod volumes were calculated as cylinders and cladocerans as elliptical disks. Other invertebrate taxa were rarely encountered and could be classified as one of the previous geometric shapes or a sphere. The tracings were measured on a digitizer, and a microcomputer automatically calculated the appropriate volumes. The coefficient of variation associated with tracing and digitizing food items was <5% (M. O. Ahlgren, unpubl. masters thesis (1984)).

Estimates of the volume of detritus and invertebrates in the gut contents were converted into estimates of AFDM with conversion factors determined by direct measurement of detritus particles and invertebrates collected from the pond. The AFDM of detritus, invertebrates, and diatoms in the foregut samples was standardized relative to fish wet weight and expressed as milligrams of diet component per gram of fish. Seasonal differences in the quantity of diet components were analyzed by a Kruskal–Wallis ANOVA and nonparametric multiple comparisons (Conover 1980).

Conversion Factors

Weight/volume conversion factors were determined on 10 groups of chironomid larvae and 4 groups of cladocerans. The volume of invertebrates in each group was determined by microscopy. AFDM was calculated as dry mass lost after combustion at 550°C for 1 h. Each group of invertebrates was dried 24 h at 105°C in preashed aluminum pans, cooled in a desiccator, weighed to 0.01 mg on a Cahn microbalance, ashed in a muffle furnace, cooled, and reweighed. The average dry weights of 125.4 μg/chironomid and 1.5 μg/cladoceran were within the range of values for these taxa reported by others (Hall et al. 1970; Dumont et al. 1975). Chironomids and cladoceran AFDM was 80 and 90% of the dry mass, respectively. The resulting conversion factors were 0.1390 mg chironomid AFDM/mm^3 and 0.0514 mg cladoceran AFDM/mm^3.

The upper 2–4 mm of detritus from the sediment surface and from submerged macrophyte leaves was drawn by suction through a latex tube into an evacuated 1-L Erlenmeyer sidearm flask and preserved in 10% formalin. The volume of detritus in each sample was determined by quantitative microscopy. AFDM of the sample was calculated after ashing dried subsamples in a muffle furnace 1 h at 550°C. Detritus ranged from 31.8 to 35.6% AFDM. The resulting AFDM/volume conversion was 0.220 mg/mm^3 ($\text{SE} = 0.0009$, $n = 5$).

A diatom conversion of 0.2419 mg AFDM/mm^3 was derived from the average AFDM reported for 11 species of diatoms (Nalewajko 1966). To calculate AFDM of filamentous diatoms such as *Fragilaria* sp., *Tabellaria* sp., and *Melosira* sp., the number of cells per filament was conducted and converted to AFDM using AFDM/cell conversions derived from Nalewajko (1966).

Invertebrate Abundance

Benthic invertebrates were sampled every 3–4 wk from April through October 1986 from the inlet bay of the pond which consistently contained the highest densities of juvenile sucker. Samples from this habitat were considered to best reflect trends in the abundance of invertebates consumed by juvenile sucker. This section ranged in width from 5 to 25 m and had a maximum water depth of 130 cm.

Samples were collected along five transects, beginning 0.5 m from shore and extending toward the center of the bay. Transects were 10 m apart. Four samples were collected at 1.5-m intervals along each transect. Samples within each transect were pooled so that each sample represented the mean of four cores. Each transect incorporated the two main habitat types in the bay: sandy shoreline *Typha* sp. beds and central silty *Potamogeton* sp. beds.

The samples were collected with Plexiglas tubes (57-mm inner diameter, 33 cm high) inserted 10–20 cm into the sediment and immediately plugged at the top and bottom with a No. 12 solid rubber stopper. The upper 10–15 mm of the sediment core and all overlying water were removed with a syphon, collected on a 250-μm sieve, and rinsed into plastic bags with 80% ethanol. A small amount of rose bengal stain was added to the ethanol to facilitate invertebrate enumeration. Invertebrates <250 μm were not collected because they comprised <5% of the invertebrate AFDM observed in sucker foregut contents.

The sample was diluted with water to a total volume of 1 L and suspended in a magnetically stirred beaker. Five 10-mL subsamples were removed from the beaker with a wide-mouth pipet and transferred to a petri plate marked with a bottom grid. The entire plate was scanned at 35 × with a binocular dissecting scope and the invertebrates were identified to subclass, order, or family.

Intentional Ingestion

To evaluate the hypothesis that juvenile sucker ingest detritus intentionally and that the quantity ingested varies inversely with the abundance of invertebrate prey, I examined foregut contents of individuals offered diets of detritus combined with four densities of brine shrimp (*Artemia*). Each diet was fed to five groups of three sucker (average 45.6 mm SL and 1.29 g wet weight) contained in aerated, 2.5-L, 18-cm bottom diameter plastic pails. Two centimetres of washed sand covered the bottom of each pail. The depth of detritus over the sand substrate was approximately 5 mm, equal to half the height of the sucker's head. This quantity of detritus greatly exceeded the amount that sucker could ingest during the experimental feeding period.

TABLE 1. Mixtures of *Artemia* and detritus presented to juvenile white sucker in aquaria.

	Ration 1	Ration 2	Ration 3	Ration 4
Artemia as % dry mass	0.09	0.04	0.02	0.0
Artemia as % AFDM	0.5	0.2	0.1	0.0
Artemia, μg dry mass/cm^2	57.3	22.9	11.4	0.0
Artemia, μg dry mass/L	5819	2328	1164	0.0
Artemia, number/L	2530	1012	506	0.0
Artemia, number/cm^2	25	10	5	0.0
Detritus AFDM as % dry-mass	18.4	18.4	18.4	18.4

Detritus was collected from the littoral zone of the study site, sieved, and the <45-μm fraction allowed to settle into a dense layer. Excess water was decanted, the detritus sample was suspended as 900 mL total volume in a beaker with a magnetic stir bar, and 45-mL aliquots were removed with a volumetric pipet and placed in beakers.

Artemia were cultured from eggs in aerated salt water for 48 h at 22°C. Live *Artemia* were rinsed with tap water and added to 45-mL aliquots of concentrated detritus at the rations listed in Table 1. Ration composition was calculated from mean values of 2.3 μg dry mass/*Artemia* ($\text{SE} = 0.03$) and 1.7 μg AFDM/*Artemia* ($\text{SE} = 0.03$) determined from nine replicate groups of 160 – 250 rinsed *Artemia* according to the procedure described above for cladoceran and chironomid conversion factors. A detritus organic content of 18.4% was determined using a muffle furnace.

The fish fed 4 h, starting at 1400, and were then killed. The entire gut was removed and preserved in 10% formalin. The AFDM of detritus present in the foreguts was determined by microscopy as previously described. *Artemia* of a uniform size were the only invertebrates ingested. Thus, the number of *Artemia* in each foregut was estimated and multiplied by 1.7 μg ADFM/*Artemia* to determine ADFM.

Sucker were observed while they fed in laboratory aquaria and in the pond. Individual maneuvers, body position, and orientation to other fish were described.

Results

Diurnal Diet Composition

No diurnal changes in diet composition or feeding intensity were evident throughout the 24-h diet survey of July 30–31, 1982. Fish with full foreguts were always captured. All fish contained detritus, 97% contained invertebrates, and 63% contained algae, mainly diatoms and desmids. Detritus consisted of amorphous particles 20–80 μm long, with occasional recognizable plant fragments. Quantities of the three food types varied widely among individuals collected at the same time (Table 2) and did not differ between sample periods, or when sample periods were combined to correspond to periods of daylight, night, dawn, and dusk (Friedman test, $p > 0.75$) (Zar 1984). Diet composition in late July 1982 was similar to that in early August 1986 (Fig. 1; Table 2). Algae was a small part of the diet AFDM (3%), while detritus (43%) and invertebrates (54%) made similar contributions to diet AFDM.

TABLE 2. Diet composition for white sucker collected throughout a 24-h period beginning on July 30, 1982. Confidence limits (95%) for mean total AFDM are 23.2–31.6.

Time	Standard length (mm)	Foregut contents (mg AFDM/g fish)	% of AFDM Detritus	% of AFDM invertebrates	% of AFDM Algae
0900	54	0.215	37.1	62.9	0.0
0900	57	0.138	39.6	57.7	2.7
0900	54	0.363	36.9	63.1	0.0
0900	60	0.183	58.2	41.8	0.0
1200	60	0.228	80.0	91.7	0.3
1200	62	0.146	72.2	26.8	0.4
1200	60	0.378	25.0	75.0	0.0
1200	66	0.646	65.8	34.2	0.0
1500	58	0.283	49.5	50.5	0.0
1500	64	0.246	68.9	31.1	0.0
1500	64	0.434	48.4	51.2	0.3
1500	66	0.525	97.2	00.0	2.8
1500	62	0.104	81.1	18.9	0.0
1800	65	0.114	47.2	47.9	4.8
1800	65	0.289	25.6	70.5	3.8
2000	62	0.130	47.7	52.3	0.0
2000	58	0.302	60.4	39.6	0.0
2000	58	0.222	33.4	66.6	0.0
2200	62	0.258	25.3	26.0	72.2
2200	62	0.261	11.9	87.4	0.6
2400	53	0.469	27.2	72.9	0.0
2400	58	0.106	36.0	96.4	0.0
2400	60	0.803	22.0	70.8	8.9
2400	62	0.237	51.4	48.6	0.0
0300	56	0.545	83.3	16.7	0.0
0300	62	0.391	54.0	94.5	0.2
0300	65	0.093	23.8	74.9	1.4
0600	65	0.091	10.9	89.1	0.0
0600	53	0.095	43.2	56.8	0.0
0600	57	0.263	83.2	16.8	0.0
Mean	60	0.274	43.1	53.6	3.3
Median	60	0.241	41.4	54.6	0.0
Range	(53–68)	(0.037–0.803)	(3.6–97.2)	(0.0–96.3)	(0.0–72.2)

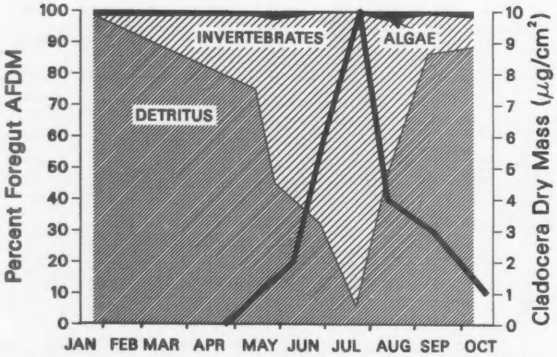

FIG. 1. Seasonal changes in diet composition of white sucker (shaded, median %AFDM, $n = 15$) and biomass of cladocerans in the sediment (solid line).

Seasonal Diet Composition

Diet composition varied significantly with season in 1986. The quantity of foregut detritus in September and October was greater than other nonwinter sample dates ($p < 0.05$, Table 3) and comprised 88 and 90% of the diet AFDM (Fig. 1). The quantity of foregut detritus in July was less than on all other sample dates ($p < 0.01$, Table 3) and accounted for only 5% of the diet AFDM (Fig. 1). Invertebrate AFDM increased consistently from January to a July peak when it comprised 95% of the diet AFDM (Fig. 1) and was greater than at all other sample dates ($p < 0.01$, Table 3). Invertebrate AFDM decreased steadily from August through October and was completely absent from the diet in January and February. Algae contributed less than 2% of diet AFDM in all seasons (Fig 1).

Benthic microcrustaceans, mainly cladocerans (Macrothricidae), comprised 100% of the invertebrate AFDM in September and October diets and varied between 80 and 90% of the invertebrate AFDM ingested at other times of the year. Similarly, benthic microcrustaceans made up 70% of the invertebrate AFDM ingested throughout the 24-h survey in 1982. Copepodite and nauplius stages of copepods accounted for <3% of the microcrustacean AFDM ingested. The remaining invertebrate AFDM consisted of chironomids and other dipteran larvae although occasional dipteran pupae, rotifers, and nematodes were observed. Several fish contained *Elodea* seeds in October but they were not a dominant diet component. Protozoan (Difflugiidae) casts were observed sporadically from July through October. It was impossible to detect naked protozoans or to distinguish empty and full casts; therefore, protozoan AFDM is included in detritus throughout this analysis.

TABLE 3. Diet composition for white sucker collected from January 29 to October 9, 1986. Data are mean standard length (SE) and median AFDM of detritus, invertebrates, and algae in sucker foreguts (range). Within each column, values followed by the same letter are not significantly different (Kruskal–Wallis ANOVA and multiple comparisons, $p \langle 0.05$).

Date	*n*	Length (mm)	mg AFDM/g fish wet weight			
			Detritus	Invertebrates	Algae	Total AFDW
Jan. 29 and 30, Feb. 24	10	42 (6.3)	0.201 c (0.06–1.74)	0.000 a (0.000–0.000)	0.002 b (0.000–0.008)	0.207 ab (0.057–1.74)
May 15	7	49 (2.8)	0.125 b 0.888–0.226)	0.016 b (0.006–0.279)	0.001 ab (0.000–0.006)	0.180 a (0.125–0.493)
May 28	15	48 (4.0)	0.154 b (0.002–0.382)	0.119 c (0.009–0.411)	0.008 ab (0.000–0.105)	0.323 abc (0.048–0.668)
June 30	10	70 (4.6)	0.103 b (0.004–0.450)	0.116 c (0.065–0.872)	0.000 ab (0.000–0.006)	0.282 abc (0.105–0.953)
July 22 and 23	15	39 (3.9)	0.020 a (0.003–0.044)	0.370 d (0.173–1.33)	0.000 a (0.000–0.004)	0.390 c (0.210–1.37)
Aug. 6 and 13	15	49 (6.4)	0.096 b (0.016–0.429)	0.093 c (0.000–0.028)	0.003 b (0.006–0.527)	0.212 ab (0.058–0.629)
Sept. 9	15	49 (6.7)	0.294 c (0.123–1.03)	0.034 b (0.003–0.178)	0.002 b (0.000–0.017)	0.357 bc (0.153–1.06)
Oct. 7 and 9	15	50 (4.0)	0.300 c (0.070–2.68)	0.033 b (0.000–0.164)	0.001 b (0.000–0.099)	0.340 abc (0.076–2.87)

TABLE 4. Availability of benthic invertebrates from April through October, 1986. Values are expressed as µg dry mass/cm^2 substrate (range) and represent the median of five replicates. Within each column, values followed by the same letter are not significantly different (Kruskal–Wallis ANOVA and multiple comparisons, $p \langle 0.05$).

Date	Chironomidae	Cladocera	Copepoda	Nauplii	Total invertebrates	Total benthic microcrustaceans
Apr. 26	99 b (50–182)	0 a (0–2)	0 a (0–8)	0 ab (0–0.1)	106 abc (51–184)	1 a (0–8)
June 9	165 b (99–198)	2 ab (1–4)	13 b (9–28)	0 c (0–0)	194 c (123–214)	16 c (10–20)
July 1	165 b (66–363)	6 d (3–9)	23 b (15–31)	0 c (0–0)	189 c (87–398)	26 c (21–37)
July 23	99 b (0–297)	10 d (3–19)	15 b (4–19)	0 bc (0–0)	118 abc (7–326)	26 c (7–26)
Aug. 12	66 a (33–66)	4 cd (3–6)	4 a (3–7)	0 a (0–0)	74 a (39–76)	9 b (6–11)
Sept. 12	165 b (66–363)	3 bc (1–4)	4 a (0–7)	0 a (0–1)	174 bc (77–368)	9 ab (1–11)
Oct. 17	99 b (33–165)	1 a (1–2)	0 a (0–0)	0 a (0–0)	106 ab (36–170)	4 ab (2–6)

Seasonal Availability of Benthic Invertebrates

The biomass of cladocerans present in the upper 10–15 mm of pond sediment peaked in late July. Throughout July, cladoceran abundance was significantly greater than during other sample dates except August (Table 4). Copepod densities appeared to peak by early July, dropped substantially after July, and remained low for the rest of the year. The biomass of chironomids greatly exceeded the biomass of benthic microcrustaceans and showed no significant seasonal variation (Table 4). Representatives of Nematoda, Oligochaeta, Ostracoda, and Rotatoria were abundant in the core samples, but were rarely ingested by sucker; therefore, they are not included in Table 4.

Selective Ingestion Experiments

Sucker ingested more detritus and less *Artemia* from experimental diets of mixed detritus/*Artemia* that provided lower *Artemia* densities (Newman–Keuls test, $p < 0.05$, Fig. 2). The AFDM of both *Artemia* and detritus ingested from diet 1 (highest *Artemia* density) differed from other diets ($p < 0.05$, Fig. 2) and comprised 99.5 and 0.5% of the ingested diet AFDM,

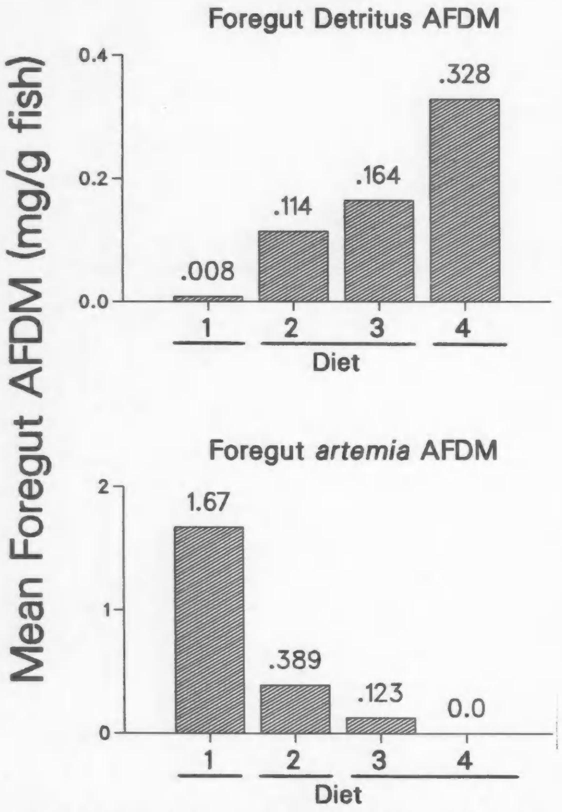

FIG. 2. Detritus, *Artemia*, and total AFDM present in the foreguts of white sucker fed detritus combined with the following rations of *Artemia* (μg dry mass/cm^2 substrate): diet 1 = 57, diet 2 = 22, diet 3 = 11, diet 4 = 0. Values connected by a line are not significantly different ($p > 0.05$).

respectively. Total AFDM ingested from diet 1 was higher than from diets 2–4 ($p < 0.05$) which did not differ. The AFDM of detritus consumed in the absence of *Artemia* was approximately 20% of the AFDM consumed by sucker fed the highest concentration of *Artemia*.

Feeding Behavior

Juvenile sucker exhibited two distinctive feeding behaviors: spitting and filtering. During the spitting maneuver, fish in the field and in laboratory aquaria aggressively bite into the sediment. This activity left distinct circular feeding marks 3–5 mm deep on the bottom of laboratory aquaria, a depth approximately half the height of the sucker's head. Sucker appeared to manipulate food inside their oral cavity before spitting debris out the mouth. Sucker in laboratory aquaria also skimmed sediment from the surface with a series of shallow bites and expelled debris from the opercular opening ("filtering").

Discussion

Detritus was a quantitatively important component of juvenile sucker foregut contents in all seasons sampled except midsummer. Seasonal variation in diet composition appears to be inversely correlated with variations in the abundance of invertebrate prey. Both laboratory and field results indicate that juvenile white sucker ingest more detritus as the availability of benthic microcrustaceans decreases. The proportion of detritus in the foreguts of sucker fed detritus mixed with different densities of *Artemia* was inversely proportional to the *Artemia* density of experimental diets. (Fig. 2). The spring shift from detritus to an invertebrate diet and the fall shift back to detritus corresponded to the summer increase and fall decrease in the abundance of benthic microcrustaceans (Fig. 1).

Changes in benthic cladoceran densities appeared to influence the sucker's diet composition more than changes in the abundance of other benthic invertebrates. Sucker consumed the greatest quantity of invertebrates during late July when cladoceran densities were greatest. Copepod abundance peaked 3–4 wk earlier at twice the cladoceran peak density. Chironomid densities did not appear to influence diet composition. Cladocera was the main invertebrate group ingested by juvenile sucker in all seasons. Others have stated that juvenile white sucker prefer cladocerans compared with copepods or benthic insect larvae (Lalancette 1977; Barton 1980). Sediment-dwelling cladocerans swim sluggishly at the water sediment interface (Brooks 1965) and are probably more vulnerable to sucker predation than strongly swimming copepods or burrowing, tube-building chrionomid larvae.

Juvenile sucker appear to ingest detritus intentionally. They entirely rejected detritus and consumed only *Artemia* from an experimental diet that provided both *Artemia* and detritus ad libitum (Fig. 2). The fact that sucker can separate detritus from the invertebrates they swallow suggests that detritus ingested from the other diets was intentional, not incidental. Alternatively, sucker may not be able to efficiently separate invertebrate prey from detritus if the density of invertebrate prey is low. In a preliminary experiment, detritus used to make the experimental diets was accidentally allowed to go anoxic; sucker rejected detritus from all diets and consumed only *Artemia*. This observation supports the idea that detritus ingested from diets with low *Artemia* densities was not incidental and therefore was ingested intentionally. Other detritus-consuming omnivorous fish consume mainly invertebrates during periods of high invertebrate abundance (Persson 1983; Weisberg and Lotrich 1986; Prejs and Prejs 1987). The seasonal absence of detritus in the diet of these fish suggests that they can also exclude detritus from invertebrates that are swallowed and that detritus is ingested by choice during periods of low invertebrate prey availability.

The spitting and filtering behaviors suggest that sucker sort food in their bucal cavity. This region appears highly adapted to discriminante and sort food items. Dense rows of sensory papillae and taste buds line the lips, mouth, gill arches, and thick fleshy palatal organ which forms the roof of the pharynx (Stewart 1926). External morphology of the brain reflects greater development of taste and touch within the oral cavity relative to the lips and skin (Miller and Evans 1965). Rows of fleshy, papillose, plate-shaped gill rakers interdigitate forming a variable meshed sieve similar to other catostomids (Weisel 1962; Dunham et al. 1979.)

Sucker appear to glean invertebrates from detritus by spitting. In response to gustatory and tactile stimuli, the gill rakers and palatal organ probably maneuver invertebrates until pinned between the palatal organ and comblike pharyngeal teeth (Eastman 1977). When the palatal organ contracts, the pharynx constricts and gill rakers, interdigitate tightly, blocking external gill openings. Unwanted debris is ejected out the mouth and invertebrates swallowed whole. Sucker appear to filter detritus through gill rakers. Filtering may enable sucker to discard large particulate debris or heavy inorganic material. Detritus particles as large as the invertebrates and sand grains were rare in gut contents.

Short-term individual variation characterizes all aspects of fish foraging behavior (Ringler 1983) and was evident in the diet composition of this sucker population over diurnal (Table 2) and seasonal cycles as evidenced by the standard error associated with diet composition of individuals collected on the same date (Table 3). Variation among individuals was greatest when invertebrate densities in the pond were intermediate and sucker ingested substantial quantities of both detritus and invertebrates. Individual variation decreased when sucker ingested primarily detritus or invertebrates (Table 3) which corresponded to periods of low and high invertebrate abundance. This pattern of variability may reflect the patchy distribution of preferred foods and opportunistic feeding by omnivorous fish. The ability to use many different foods effectively is an important characteristic of ubiquitous species (Lowe-McConnell 1975, p. 210) and has probably contributed to the white sucker's widespread distribution.

Juvenile sucker appear to gorge themselves on unlimited invertebrates but not on detritus. They ingested 5 times more AFDM from experimental diet 1 (ad libitum *Artemia* and detritus) than sucker fed diet 4 (ad libitum detritus alone). The total AFDM consumed by sucker in the pond was similar to the AFDM ingested from diets 2–4 but much lower than that ingested from diet 1 (Fig. 2; Table 3). The *Artemia* biomass provided by diet 1 may have been unnaturally high and could explain the apparent discrepancy between the maximum AFDM consumed by fish fed diet 1 and fish in the pond. The *Artemia* biomass provided by diet 1 was approximately 2 times greater than the highest microcrustacean biomass value measured in the pond. However, the *Artemia* biomass in diets 2–4 was similar to the microcrustacean biomass measured in the pond (Tables 1 and 4). The limited availability of invertebrate prey in the pond may have prevented sucker from gorging on invertebrates. Alternatively, *Artemia* provide approximately 4 times more AFDM per unit dry weight than detritus. A foregut filled with *Artemia* would be expected to contain much more AFDM than one filled with detritus.

There are several reasons why sucker may not gorge on detritus. Specific amino acids are known to stimulate short-term appetite in fish (Fletcher 1984). Detritus typically contains low concentrations of amino acids (Bowen 1987) and may not strongly stimulate appetite. Many gustatory and olfactory stimuli inhibit fish feeding (Fletcher 1984). The fraction of fine particulate detritus derived from fragmentated plant debris retains secondary metabolites such as phenolic acids which may deter feeding through changes in acidity or noxious flavors they give detritus (Valiela and Rietsma 1984). Although copious quantities of detritus are always present, the quantity of palatable detritus may be limited.

Detritus typically contains much less protein and energy per unit AFDM than invertebrates and is less digestible (Bowen 1987). Assimilation efficiencies determined for a variety of aquatic detritivores averaged 0–40% whereas invertebrates are usually assimilated with 80–100% efficiency (Valiela 1984). Although the efficiency with which sucker assimilate nutrients from detritus relative to invertebrates has not been well studied, invertebrates appear to be a higher quality food than detritus. The fact that sucker clearly prefer invertebrates is not surprising; however, the fact that they choose to ingest detritus at certain times of the year suggests that detritus is nutritionally valuable. The exact nature of this nutritional benefit is unknown.

Most energy and materials in freshwater and marine ecosystems enter food webs as detritus rather than as living plant material (Mann 1988). Studies of the trophic basis of fish production have often overlooked the potential direct contribution of detritus to fish production and have focused on benthic invertebrates as necessary intermediates in the conversion of detritus to fish biomass (Lotrich 1973; Horwitz 1978; Eggers et al. 1978; Boisclair and Leggett 1985). Results presented here show that juvenile white sucker ingest detritus intentionally and that detritus can comprise a large part of the diet when invertebrate prey are the least abundant. Future studies that assess the nutritional contribution of detritus to the diet and its ability to support the growth of white sucker as well as other fish species are necessary for a more complete understanding of the trophic basis of fish production.

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Nutritional Significance of Facultative Detritivory to the Juvenile White Sucker (*Catostomus commersoni*)

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The nutritional significance of detritus in the diet of the juvenile white sucker (*Catostomus commersoni*) was evaluated by experiments designed to assess assimilation efficiency and growth of sucker fed detritus and other foods. Sucker in laboratory aquaria assimilated detritus with the following efficiencies: dry mass = 19.6%, ash-free dry mass (AFDM) = 59.7%, total amino acids = 68.9%, energy = 69.4%. Assimilation efficiencies calculated for invertebrates and natural field diets were slightly higher. Diatom assimilation was low (5.5%). In growth experiments, sucker fed detritus ad libitum lost weight, while those fed *Artemia* ad libitum grew rapidly. However, detritus increased the growth rate of sucker fed a limited invertebrate ration and reduced the rate of weight loss relative to unfed fish. The ratio of digestible protein to digestible energy calculated for natural detritus diets (3.2 mg amino acid/kJ) indicates that the protein content of detritus is too low to support growth. Detritus provides energy which complements limited invertebrate protein to enhance growth or reduce the rate of weight loss when invertebrate prey are not available.

L'importance nutritive des détritus dans le régime alimentaire du jeune Meunier noir (*Catostomus commersoni*) a été évaluée au moyen d'expériences visant à établir l'efficacité d'assimilation et la croissance des Meuniers nourris de détritus et d'autres aliments. Les Meuniers des aquariums de laboratoire assimilaient les détritus à raison des valeurs suivantes : masse sèche = 19.6 %, masse sèche sans cendre (AFDM) = 59.7 %, acides aminés totaux = 68.9 %, énergie = 69.4 %. L'efficacité d'assimilation calculée pour les invertébrés et les régimes naturels sur le terrain était légèrement supérieure. L'assimilation de Diatomés était faible (5.5 %). Dans les expériences de croissance, les Meuniers nourris de détritus à volonté ont perdu du poids tandis que ceux nourris de *Artemia* à volonté ont connu une croissance rapide. Toutefois, les détritus ont augmenté le taux de croissance des Meuniers nourris d'une ration d'invertébrés limitée et réduit le taux de perte de poids des poissons non nourris. Le ratio protéines digestibles : énergie digestible calculé pour les régimes de détritus naturels (3.2 mg acide aminé/kJ) révèle que la teneur en protéines des détritus est trop faible pour soutenir la croissance. Les détritus fournissent une énergie qui complète un apport limité de protéines d'invertébrés pour favoriser la croissance ou réduire la rythme de perte de poids lorsque les proies invertébrées ne sont pas disponibles.

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Most aquatic animals, including fish at all trophic levels, consume detritus at some stage of their life cycle (Darnell 1964). Detritus is fully adequate to support growth of detritivorous fish (Bowen 1979, 1981; Lewis and Peters 1984) but its nutritional significance in the diets of omnivorous fishes has been repeatedly questioned and detritus is often considered to be ingested incidentally with animal material (Prinslow et al. 1974; Kneib et al. 1980; Lin et al. 1981; Weisberg and Lotrich 1982, 1986).

Recent work has shown that the omnivorous juvenile white sucker (*Catostomus commersoni*) ingests detritus intentionally and that the quantity of detritus in its diet varies inversely with invertebrate prey abundance. Detritus contributed 80–100% of the ash-free dry mass (AFDM) in the sucker's diet during periods of low benthic invertebrate standing stock (Ahlgren 1990). The fact that detritus is an intentional and quantitatively important component in the white sucker's diet suggests that it is nutritionally valuable. This possibility was investigated in the work reported here.

Two approaches are commonly used to assess the value of food to consumers. Each has advantages and limitations. An empirical approach in which growth rates are measured for consumers fed different diets provides data that have immediately apparent biological relevance. The nutritional benefit from any food is ultimately realized by its contribution to the consumer's fitness. Growth of fish is considered to closely approximate fitness because increased size reduces vulnerability to predators, increases feeding efficiency, and increases reproductive output. Growth, however, is an inappropriate food value index for foods which lack certain essential nutrients. These foods alone will not support somatic growth and their partial contribution to the consumer's total nutrition may be overlooked. Also, growth rates are affected by species, age, temperature, and other environmental variables and are not directly comparable as a predictive food value index if these variables are not controlled.

An alternative approach is to measure the quantity of assimilable nutrients in the food type. This approach is based on absolute units that have predictive value and are directly comparable among other food quality studies. The significance, however, of a particular nutrient to the consumer's fitness is implied. The biological relevance must be validated.

The nutritional significance of detritus in the diets of omnivorous fish will be understood best by a combination of these two approaches. This study assesses the juvenile white sucker's ability to (1) assimilate organic matter, protein, and energy from detritus and other diet components and (2) grow on detritus, invertebrate, and mixed detritus/invertebrate diets. The nutritional significance of detritus for the white sucker, indicated by growth experiments, is interpreted in terms of how detritus helps the consumer meet its needs for protein and energy.

Methods

All fish were collected by seine from a pond in Houghton Co., MI (described by Ahlgren 1990).

Laboratory Assimilation Experiments

Assimilation efficiencies of sucker fed detritus, diatoms, and invertebrates were assessed in laboratory aquaria. Fish were acclimated to laboratory conditions 2–3 wk on a mixed diet of commercial pelleted trout food, detritus, and *Artemia* diet.

Three types of invertebrates were tested: daphnia, simuliid, and meal worm larvae. Groups of 10–25 fish (70 mm mean standard length (msl)) were placed in clean, aerated, 11-L aquaria along with the invertebrate under investigation. The fish fed ad libitum 4–8 h and were transferred to an aquarium fitted with a plastic screen which excluded fish from the bottom. Feces dropped below the screen and remained in discrete strands. Feces were removed with a pipet 2–12 h after defecation, dried for 4 h at 110°C, and stored in glass vials. The feeding process continued 1–2 wk with feces from each day stored separately and three or four replicate trials conducted per food type. Samples of each type of invertebrate were dried and stored in glass vials.

Detritus was collected daily from the surface of pond sediments and macrophytes at <1 m depth. The upper 2.5 cm of sediment was removed with a plastic container. Macrophytes were carefully uprooted, placed in a pail with pond water, and agitated to dislodge detritus. All detritus was poured through a 45-μm sieve to remove macrophyte debris and macroinvertebrates and allowed to settle 30 min. The supernatant was poured off and the remaining thick slurry was fed to three groups of 40 sucker (48 mm msl) for 2 wk and one group of 10 sucker (95 mm msl) for 3 wk. The fish were contained in aerated, glass aquaria with 11 L of water. Fecal samples were collected daily as described above. On the last day of each feeding trial the fish fed 3–4 h and were killed. Contents in the foregut (anterior one fifth of the gut (Ahlgren 1990)) were extruded, dried, and stored as pooled samples by groups.

Diatoms were obtained from a laboratory culture, mixed with detritus to obtain a workable volume of food, and fed ad libitum for 6 d to groups of 5 fish (88 mm msl) and 10 fish (52 mm msl) contained in aerated 2.5-L aquaria. The fish were fed the diatom/detritus mixture daily for 6 d. The fish were killed and their guts excised and fixed in 10% formalin. The proportion of diatom frustules with visible cytoplasm, present in formalin-preserved samples of foregut and hindgut contents, was determined by the light microscope technique of Lund et al. (1958).

Assimilation by Fish in Their Natural Habitat

Assimilation of natural diets was determined from gut and fecal samples collected from fish in the pond. Sucker (77 mm msl) were collected on August 5 and 6 and October 3, 11, and 17, 1985. Fish were killed, guts excised on site, and contents removed from the foregut and hindgut which was divided into thirds. Contents from each section were placed in separate foil pans. Each pan contained contents from seven fish. Samples were dried to a constant weight at 110°C. Ten fish were transported to the laboratory and held in the defecation aquarium overnight. Feces were collected and dried at 110°C. Additional guts from each sample session were preserved in 10% formalin and analyzed by quantitative microscopy (Ahlgren 1990) to assess diet composition.

Chemical Analyses

All dried samples were ground to a fine powder. Organic content was estimated as AFDM determined by weight loss after ignition at 550°C in a muffle furnace (Ahlgren 1990). Hydrolysis-resistant organic matter (HROM), mainly cellulose and chitin, was determined according to Buddington (1980). The residue was dried, weighed, and ignited at 550°C for 1 h to determine hydrolysis-resistant ash (HRA), mainly ash that is insoluble under acid digestion (Bowen 1981). Energy content was determined by oxygen microbomb calorimetry (Cummins and Wuycheck 1971). Amino acids were freed by acid hydrolysis under nitrogen (24 h). Recovery of amino acids after hydrolysis was assumed to be 100%. Total amino acid content of samples obtained in the detritus feeding experiment was quantified by a fluorimetric technique calibrated with glycine (Bowen 1980). Total amino acid content of samples obtained from fish in the field was quantified with an automated amino acid analyzer.

Calculation of Assimilation Efficiency (%AE)

Assimilation efficiency (%AE = amount of food removed by the gut as a percentage of that ingested) was calculated by Conover's (1966) indigenous dietary marker method. HRA was the marker in detritus and field diets. HROM was the invertebrate marker, since the quantity of HRA in the feces of sucker fed invertebrates was too small to measure precisely. Nutrient content of feces and dried invertebrates was compared in invertebrate %AE calculations. Because sucker were suspected to selectively ingest the organic fraction of detritus (Ahlgren 1990), detritus %AE calculations compared nutrient density of feces with foregut contents rather than detritus. Assimilation of the field diet was calculated by comparing foregut contents with feces and also with hindgut samples. Assimilation of total dry mass and organic matter was calculated for all samples. In addition, assimilation of amino acids and energy content was determined for detritus fed to sucker in aquaria and for natural diets. Diatom assimilation was calculated as the decrease in the percentage of diatoms with chloroplasts between the foregut and hindgut.

Growth Experiment

A feeding experiment was conducted during October 1987 to determine standard growth rates of juvenile white sucker fed detritus (ad libitum), invertebrates (ad libitum), limited invertebrates (invertebrate dry weight fed at 0.5% of fish wet weight per day), limited invertebrates plus detritus (ad libitum), and unfed fish. Sucker (1.4 g wet weight ± 0.08 SD) were collected from a population previously shown to shift from a diet of invertebrates to detritus during this time of the year (Ahlgren 1990) and acclimated to experimental conditions for 1 wk on a detritus/trout pellet diet.

The <250-μm fraction of detritus was collected by the procedure described previously. This size fraction excluded invertebrates commonly ingested by 1.4-g sucker (Ahlgren 1990). Excess detritus was frozen and fed to fish on days when weather conditions made collecting fresh detritus unfeasible. Live *Artemia* rinsed with tap water served as the invertebrate source. Brine shrimp (*Artemia*) were cultured from eggs in aerated salt water for 48 h at 22°C.

A total of 75 fish were used in a completely randomized experimental design with five treatments and five replicates per treatment. To accommodate juvenile sucker's gregarious behavior, each replicate consisted of three fish. The diets were fed 3 times per day for 21 d. Fish were contained in 2.5 L of conditioned water in white plastic tanks. The tanks were aerated, photoperiod was maintained on a 14 : 10 light : dark cycle which approximated natural conditions, and water changed daily. Water was carefully removed with a syphon and added through a standpipe in the center of each tank. Water for all treatments was conditioned in a holding tank containing goldfish and microbially colonized undergravel filters.

Fish were weighed on days 1 and 21. Individuals were blotted on a damp sponge for 5 s to remove surface water and were placed inside a cup containing 75 mL of water tared to zero on a top-loading balance. Weight was read to 0.01 g. The combined weight of three fish in each bucket was considered a sample unit and used to calculate specific growth rate (SGR) from the following equation (Ricker 1979):

$$\mathrm{SGR}\ (\%/\mathrm{d}) = \frac{(\ln W_2 - \ln W_1)}{t} \times 100.$$

SGR produced by the five diets was compared with a Student–Newman–Keuls test and multiple contrasts (Zar 1984).

Results and Discussion

Assimilation Efficiency (%AE)

Juvenile white sucker assimilated 59.7% of detrital organic matter (AFDM) consumed during laboratory experiments (Table 1). These values are similar to %AE estimated for omnivorous gizzard shad (*Dorosoma cepedianum*) fed natural detritus (Mundahl and Wissing 1988) and are within the range (20–75) of %AE estimated for exclusively detritivorous fish in their natural habitat (Bowen 1981; Lewis and Peters 1984; Nelson and Wilkins 1988). Assimilation of detrital amino acids by sucker (68.9%, Table 1) is similar to assimilation of detrital protein (72.2%) and nonprotein amino acids (63%) by detritivorous *Tilapia* (Bowen 1981). Sucker assimilated detrital energy as efficiently (69.4%) as detrital amino acids (Table 1).

Juvenile sucker, like other fish, assimilated animal foods more efficiently than plant foods (Table 1). %AE determined for sucker that were fed invertebrates in laboratory aquaria ranged from 66 to 79% of invertebrate AFDM (Table 1) which is lower than the range of %AE (78–97%) reported for other fish fed invertebrates with chitenous exoskeletons including other stomachless omnivorous fish (Targett 1979; Weisberg and Lotrich 1982), stomachless carnivorous fish (Atmar and Stewart 1972), and fish with gastric stomachs (reviews in Conover 1978; Pandian and Vivekanandan 1985).

During August, sucker in the pond assimilated a mixed diet, composed of 60% invertebrate AFDM and 40% detritus AFDM, more efficiently than they assimilated invertebrates in the laboratory (Table 1). Assimilation of the August diet AFDM (81.7%) was similar to %AE determined for other fish fed invertebrates. Foregut samples pooled from three weekly sampling trips in October resulted in an overall AFDM composed of 70% detritus and 30% invertebrates. Assimilation of AFDM, amino acids, and energy was 12, 9, and 10% lower in October than in August (Table 1) and reflects the higher detritus content of the October diet.

Nutrient loss from feces due to leaching increases %AE estimates of dry weight, protein, and nitrogen by approximately 10% (Windell et al. 1978; Smith et al. 1980). Two-sample *t*-tests showed that %AE estimates of the August field diet which were calculated from the nutrient content of foregut and feces samples were 7–10% greater ($p < 0.05$) than estimates based on foregut and hindgut samples. Although laboratory estimates of %AE were subject to error associated with nutrient leaching from feces, they appear to be conservative. Daily handling stress associated with feces collection may have reduced %AE during laboratory experiments.

TABLE 1. Percent assimilation efficiency (%AE) of white sucker for total dry mass, ash-free dry mass (AFDM), total amino acids, and energy content in detritus, invertebrates, and natural diets. Values are mean ± SE (*n*).

Sample	Dry mass	AFDM	Amino acids	KJ energy
		Feeding experiments		
Detritus[a]	19.6 ± 1.7 (7)	59.7 ± 2.9 (7)	68.9 ± 5.8 (3)	69.4 ± 0.4 (3)
Simuliidae[b]	60.5 ± 1.4 (3)	77.9 ± 1.3 (3)	—	—
Daphnia[b]	54.9 ± 1.7 (3)	66.0 ± 1.2 (3)	—	—
Meal worms[b]	65.1 (1)	66.9 (1)	—	—
		Field diets, 1985		
Aug. 5–6[a]	77.3 ± 2.5 (5)	92.0 ± 0.8 (5)	97.9 ± 0.1 (3)	92.2 ± 0.2 (3)
Aug. 5–6[b]	68.2 ± 2.4 (5)	81.7 ± 2.3 (5)	88.2 ± 2.3 (3)	85.4 ± 2.4 (3)
Oct. 3, 11, 17[c]	42.5 (1)	69.3 (1)	78.9 (1)	75.5 (1)

[a] % AE calculated from foregut and fecal samples.

[b] % AE calculated from dried invertebrate and fecal samples.

[c] % AE calculated from foregut and hindgut samples.

TABLE 2. Starting weight (Wt_0), final weight (Wt_{21}), and specific growth rate (SGR) of groups of three white sucker fed five diets for 21 d. Data are mean (SE), $n = 5$. Means followed by different letters do not differ (Student–Newman–Keuls multiple range comparison, p ⟨0.01). Final mean standard length = 45.4 mm (SE = 0.04, $n = 75$).

Diet	Wt_0 (g)	Wt_{21} (g)	SGR (%/d)
Artemia (ad libitum)	3.80 (0.09)	5.21 (0.16)	1.50 (0.14) a
Detritus (ad libitum) + *Artemia* (limited)	4.18 (0.47)	4.02 (0.46)	−0.19 (0.07) b
Artemia (limited)	4.24 (0.63)	3.72 (0.31)	−0.65 (0.10) c
Detritus (ad libitum)	3.86 (0.06)	3.36 (0.08)	−0.66 (0.09) c
Unfed	4.16 (0.13)	3.24 (0.11)	−1.19 (0.07) d

Assimilation of diatoms was low. The percentage of diatom frustules with intact chloroplasts decreased between the foregut and the hindgut (Wilcoxon's signed rank test, $p < 0.015$) by only 5.5% ($n = 15$, SE = 0.67). Atmar and Stewart (1972) found that diatoms passed undigested and viable through the gut of the stomachless top minnow (*Fundulus notatus*). Diatoms are readily digested by the cichlids *Tilapia mossambicus* (Bowen 1979) and *T. nilotica* (Moriarty and Moriarty 1973). Both *Tilapia* species possess true stomachs which can create unusually acid conditions (pH < 2.0). Acid gastric secretions in *Tilapia* effectively lyse bacteria and blue-green algae cell walls and denature diatom cell membranes (Bowen 1982). The secretions appear to facilitate digestion more effectively than the intestinal fluids of stomachless fish.

Growth

SGR differed for sucker fed all diets except the ad libitum detritus and limited *Artemia* ($p < 0.01$, Table 2). The range of SGR observed in this study (−1.19 to +1.5) is within the range of values reported in other laboratory growth experiments for unfed fish and fish fed limited rations and rations designed to produce maximum growth (Prinslow et al. 1974; Weisberg and Lotrich 1982; Bowen 1987). As expected, the ad libitum *Artemia* diet produced weight gain, the limited *Artemia* ration produced weight loss, and the starved fish exhibited severe weight loss. The ad libitum detritus diet did not produce positive growth: however, it produced significantly less weight loss compared with unfed fish. A combination of the limited *Artemia* ration and ad libitum detritus produced a greater SGR than either diet alone.

Although detritus did not produce positive growth, it contributed positively to the sucker's diet by complementing the limited *Artemia* ration and slowing weight loss. Other studies have shown that detritus alone will not support the growth of detritus-consuming omnivorous fish. However, the nutritional contribution of detritus to fish in these studies is unclear. Prinslow et al. (1974) measured the growth of mummichogs (*Fundulus heteroclitus*) fed different rations of commercial fish food alone and supplemented with salt marsh detritus. Mummichogs that were fed detritus did not gain weight but nitrogen retention in their body tissues increased. Detritus appears to have enhanced the growth response in six of the seven treatments. The difference, however, was not significant ($0.10 < p < 0.15$). Similarly, silver carp (*Hypophthalmichthys molitrix*) did not grow when fed *Microcystis* detritus, although they lost less weight than unfed fish (Lin et al. 1981). Mundahl and Wissing (1987) observed poor growth and condition of gizzard shad during periods of the year when they consumed detritus. Overall growth and condition of fish in their study were less than in populations of gizzard shad that fed heavily on live foods. Whether consumption of detritus by gizzard shad was better than starving cannot be assessed.

Nutritional Significance

The fact that detritus does not appear to produce growth in omnivorous fish has often been interpreted to mean that detritus provides little nutritive value (Prinslow et al. 1974; Kneib et al. 1980; Lin et al. 1981; Weisberg and Lotrich 1982, 1986). This view is misleading because it implies that all foods are qualitatively similar. An alternative explanation is that detritus is deficient in certain essential nutrients provided by invertebrates. Differences in the food quality of detritus and invertebrates must be identified to understand the nutritional contribution of detritus to the white sucker's diet.

Protein or total amino acids and digestible energy have been suggested as the most important determinants of food quality for aquatic animals feeding on natural diets (Bowen 1987). Other nutrients such as vitamins, minerals, and specific lipids and amino acids also affect growth. However, they are required in small quantities by weight, and deficiencies would not be expected to affect short-term growth (National Research Council 1977). Microorganisms associated with natural diets can also provide a rich source of supplemental nutrients such as vitamins (Cummins and Klug 1979).

The ratio of digestible protein to digestible energy provides a biologically meaningful food quality index for primary consumer fish (Bowen 1982). Protein is generally considered to be the main limiting nutrient in plant material and detritus (Vaughan 1978; Persson 1983; Hofer et al. 1985). Appetite in fish is controlled by metabolic energy needs and gut fullness (Talbot 1985). Hence, the relative concentration of dietary protein to energy controls the amount of protein consumed. At a physiological level, protein and energy interact in a complex fashion to determine growth. Amino acids provide the fundamental structural components of animal tissue and may also provide energy. Although excess energy can be used to synthesize certain amino acids, 10 essential amino acids cannot be synthesized and must be provided by the diet. If the energy content of the diet is inadequate, dietary protein will be catabolized to meet metabolic energy needs and will not provide materials for growth. Based on the similarity across animal taxa of the amount of organic nitrogen required for growth (Russel-Hunter 1970), Bowen (1979, 1982) proposed that about 4.3 – 5.3 mg digestible protein/kJ digestible energy is required for maintenance, while maximum growth occurs between 20 and 30 mg/kJ.

The amino acid content of detritus is much lower than that of invertebrate larvae (Table 3). Detrital organic content, total amino acids, and energy content (Table 3) are within the range of values reported for a variety of marine and freshwater detritus samples (Bowen 1987). Values for the three invertebrate taxa (Table 3) are typical of other aquatic insect larvae (Yurkowski and Tabachek 1978).

According to Bowen's criteria, the protein to energy ratio of pond detritus (3.2 mg digestible amino acids/kJ digestible energy, Table 3) is too low to support somatic growth. The protein to energy ratio of invertebrates (25.7 mg amino acid/kJ) is within the range of values expected to support maximum growth. These values are consistent with the observation that sucker fed to satiation on invertebrates grew rapidly whereas sucker fed to satiation on detritus did not grow. Others have

TABLE 3. Organic matter, total amino acid (AA), and energy (KJ) content of representative freshwater invertebrates and detritus fed to white sucker during an experiment designed to assess growth produced by these diets.

		Total		Assimilable		
	% organic	mg AA/ 100 mg AFDM	kJ/ g AFDM	mg AA/ 100 mg AFDM[c]	kJ/ g AFDM[c]	mg AA/ kJ
Daphnia *pulex*	80.7[a]	51.0[a]	18.73[b]	44.9	15.9	28.2
Diaptomus sp.	94.2[a]	61.7[a]	23.41[b]	54.3	19.9	27.3
Chrionomidae	90.8[a]	52.5[a]	25.31[b]	46.2	21.5	21.5
Mean (SE)	88.6 (4.0)	55.1 (3.3)	22.5 (2.0)	48.5 (2.9)	19.1 (1.7)	25.7 (2.1)
Detritus (Sept. 22, 1987)	16.1	6.1	18.52	4.2	12.8	3.3
Detritus (Sept. 23, 1987)	20.7	4.6	17.81	3.2	12.3	2.6
Detritus (Sept. 24, 1987)	17.3	1.9	13.96	1.3	9.6	1.3
Detritus (Sept. 27, 1987)	12.8	4.3	12.25	3.0	8.4	3.6
Detritus (Sept. 30, 1987)	13.0	6.8	13.00	4.7	9.0	5.2
Detritus (Oct. 5, 1987)	16.4	4.2	14.00	2.9	9.7	3.0
Mean (SE)	16.0 (1.2)	4.7 (0.7)	14.9 (1.1	3.2 (0.5)	10.3 (0.7)	3.2 (0.5)

[a] Derived from Yurkowski and Tabachek (1978).

[b] Cummins and Wuycheck (1971).

[c] Calculations based on %AE of invertebrate amino acids (88%), invertebrate energy (85%), and detrital amino acids and energy (69%) (Table 1).

suggested that plant material or detritus supplies inadequate protein to omnivorous fish (Vaughan 1978; Persson 1983; Hofer et al. 1985) and must be supplemented with animal matter. This view identifies a qualitative limitation of detritus food value and establishes the nutritional value of small quantities of animal protein in the diets of detritus-consuming omnivores.

However, the nutritional significance of detritus to an omnivore like the juvenile white sucker is more clearly understood from an alternative perspective. Failure of the limited *Artemia* ration to support sucker growth suggests that the potential nutritional value of high-quality foods may not be realized if their quantity is limited. When invertebrate abundance is low, invertebrates may not provide enough energy to support somatic growth even though they are a rich source of protein. In the absence of adequate dietary energy from nonprotein sources, protein is broken down to provide energy rather than to provide structural materials for growth. Protein is an inefficient energy source because a considerable protion of the energy is lost in excreted ammonia (Hofer et al. 1985). The quantity of benthic invertebrates consumed by juvenile white sucker in their natural habitat is variable and often extremely low in winter (Hall et al. 1970; Ahlgren 1990). Sucker consume detritus facultatively during periods of low invertebrate abundance. Detritus, although low in amino acids, provides a consistently abundant energy source which can complement limited invertebrate protein to enhance growth or reduce the rate of weight loss by starvation.

This detritus–invertebrate synergism is the key to understanding the significance of facultative detritivory to the juvenile white sucker. Conventional approaches to foraging theory which describe food value in terms of energy yield per unit handling time (review in Schoener 1971; Stephens and Krebs 1986) or nutrient density per unit energy (Bowen 1982) do not adequately describe the nutritional interaction of detritus and invertebrates in the sucker's diet. Rapport (1980) proposed a microeconomic modeling approach to study foraging for complementary resources to achieve a balanced diet. He showed that reproduction of the protozoan *Stentor coeruleus* was greater on a mixture of two prey species than on either species alone. The complementary quality of the mixed diet is not explained; however, nutrient balance is inferred. In the sucker's diet, the balance between detritus and invertebrates is not between complementary nutrient resources but between complementary protein and energy resources. The constraint limiting the food value of invertebrates is quantitative (inadequate energy), not qualitative (nutrient imbalance). However, quality rather than quantity of detritus appears to limit its nutritional value to aquatic consumers.

The direct contribution of detritus to the production of north-temperate freshwater fish has far reaching management implications. Catostomids are often considered detrimental to game fish because they both eat some of the same foods and could potentially compete with each other if food is limiting (Holey et al. 1979; Hayes 1988; Magnan 1988). However, the consequences for predatory game fish that compete with nongame fish for live animal foods are probably reduced if some nongame species can utilize detritus as a supplemental food source. Sucker may actually enhance the sportfishery by converting detritus, which game fish cannot eat, into juvenile sucker which game fish do eat. This study suggests that the functional role of the white sucker and other facultative detritivores in north-temperate fish communities may require reassessment.

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Assessing the Potential Extent of Damage to Inland Lakes in Eastern Canada due to Acidic Deposition. I. Development and Evaluation of a Simple "Site" Model

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Large scale aquatic effects of acidic deposition have become a prominent environmental issue in North America and Europe. Models are required to assess the potential future impacts of current levels of acidic deposition, and the potential benefits of emission controls. This paper presents a model that uses measurements of current lake chemistry and assumptions about the processes governing acidification, to first estimate original (i.e. preacidification) lake chemistry and then predict the eventual chemistry expected given a specified level of acidic sulphate deposition. The model is deliberately kept simple, so that its input requirements are modest and thus can be met on a regional scale. When applied on a regional scale the model predicts the expected eventual distributions of alkalinity and pH. Application of the model is illustrated for a watershed in north-central Ontario, which includes the area immediately to the south and west of Sudbury. Model-based estimates of current alkalinity are very similar to observed alkalinities. The predicted eventual alkalinity distributions, given current levels of deposition, indicate a trend towards recovery, consistent with other observations in the Sudbury region. A sensitivity analysis of the model indicates that its outputs are highly sensitive to estimates of preacidification lake sulphate levels, and less so to assumptions about the catchment's ability to neutralize incoming acidity. Simple, regional models such as the one presented in this paper should play a more central role than they presently do both in assessment and in the definition of future research and monitoring needs.

Les importantes répercussions des précipitations acides sur le milieu aquatique font les manchettes en Amérique du Nord et en Europe. Des modèles sont nécessaires pour évaluer les incidences potentielles futures des niveaux actuels de précipitations acides et les avantages potentiels d'une limitation des émissions. On présente un modèle qui utilise des quantifications des facteurs chimiques actuels de lacs et des hypothèses sur les processus réglant l'acidification afin d'obtenir une estimation des facteurs chimiques originaux (i.e. préacidification) et de prédire la chimie éventuelle étant donné un niveau déterminé de précipitations de sulfate acide. La simplicité du modèle est voulue afin que le nombre de données nécessaires pour son utilisation soient faibles et qu'elles puissent être obtenues au niveau régional. Appliqué au niveau régional, le modèle prédit la distribution éventuelle de l'alcalinité et du pH. On applique le modèle à un bassin versant du secteur centre-nord de l'Ontario qui comprend la région immédiatement au sud et à l'ouest de Sudbury. Les estimations de l'alcalinité actuelle obtenues du modèle sont très semblables au niveau d'alcalinité observé. Les distributions de l'alcalinité éventuelle prédite en fonction des niveaux actuels de précipitations révèlent une tendance vers le rétablissement; ceci s'accord avec d'autres observations effectuées dans la région de Sudbury. Les résultats d'une analyse de sensibilité du modèle révèlent qu'ils sont très sensibles aux estimations des teneurs en sulfate avant l'acidification du lac; par contre, ils sont moins sensibles aux hypothèses sur la capacité du bassin d'alimentation à neutraliser les apports d'acide. De simples modèles applicables au niveau régional tels que présentés devraient jouer un rôle plus crucial qu'à l'heure actuelle pour ce qui est de l'évaluation et de l'établissement des besoins futurs en recherche et en contrôle.

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What are the present or potential impacts of acidic deposition on the freshwater and fishery resources of eastern Canada? Resource managers, research directors, international negotiators, and the Canadian public all need scientific, defensible, answers to this question. Defensible estimates of potential resource loss require the development of simple, but credible, models of the effects of acidic deposition on water quality and aquatic biota.

To date, models of the effects of acidic precipitation on aquatic systems fall into two broad groups:

(1) Empirical models to predict the regional impacts of current or altered levels of acidic deposition on surface water chemistry (Henriksen 1979, 1980; Minns 1981; Thompson 1982; Wright 1983); and
(2) Detailed mechanistic models which simulate many watershed and lake processes, and attempt to mimic the behaviour of particular, intensively studied watersheds (Christophersen and Wright 1981; Schnoor et al. 1982; Chen et al. 1983; Cosby et al. 1985).

Empirical models, though yielding predictions of regional scale impacts on surface water chemistry, do not include an explicit representation of the processes involved. Therefore it is difficult to refine components of the model as new knowledge becomes available. Detailed simulation models avoid this shortcoming, but typically require inputs or calibration procedures that make regional scale application impractical. (One exception to this general rule is the simplified, regional version of the MAGIC model (Cosby et al. 1985), as developed by Hornberger et al. (1986)). Furthermore, none of these models include consideration of effects on biota.

There is a need for a model that forms a bridge between these two classes of models: a model that represents the biophysical system simply (so that it can be applied on a regional basis), but mechanistically (so that new information can be easily incorporated into the model). This is the first of a series of papers in which we present such a model. In this paper we describe the model's structure in detail, illustrate its application to a region in north-central Ontario, and briefly consider its sensitivity to uncertainty in two key input parameters. In an accompanying paper (Jones et al. 1990) we apply the model on a large regional scale and predict the consequences of proposed control strategies on the aquatic resources of eastern Canada. Subsequent papers are being prepared which will present a more detailed analysis of the uncertainties in the regional model (M. L. Jones, unpubl. data), and introduce a biological (fisheries) effects component (C. K. Minns, unpubl. data).

Model Structure

We designed the model to be simple enough to use available information to estimate potential impacts on biota across all of eastern Canada, amenable to analyses of the uncertainty inherent in such estimates, and easy to use for evaluating the effects of changes in levels of acidic deposition. The overall model consists of both a single lake, site model and a multiple lake, regional model (Fig. 1). The regional model is described in the accompanying paper (Jones et al. 1990) and is only discussed briefly here. The site model consists of a set of equations to predict the eventual chemical status of a single lake (alkalinity, pH, cations and sulphate), based on its watershed's morphometry and runoff, current chemistry of the lakewater, observed or assumed levels of sulphate deposition, and assumed values of three parameters describing acid neutralization in watersheds, sulphate reduction in lakes, and background or original sulphate. The derivation of the chemistry model is similar to that for the models developed by Henriksen (1979, 1980); Thompson (1982); Wright (1983); and Small and Sutton (1986), but has a few important differences.

The model is structured to simulate sulphur deposition; deposition of nitrate and ammonium are assumed to have no net acidifying effect. Nitrate uptake by plants and denitrification by bacteria are alkalinity-generating processes, while ammonium uptake and nitrification by bacteria are acidifying (Schnoor et al. 1983). Because most watersheds retain high proportions of both nitrate and ammonium deposition (Scheider and Dillon 1982), the difference between alkalinity-generating and acidifying nitrogen processing reactions is likely in most cases to be small, with no significant net alkalinization or acidification. However, in watersheds that do not retain all deposited nitrate (e.g. those with soils that are naturally nitrogen-rich due to the presence of nitrogen-fixing plant species (Van Migroet and Cole 1984), those that have been fertilized, or those receiving excessive atmospheric nitrogen input (Van Breeman et al. 1983)), our assumption of no effects from nitrogen deposition may lead to underestimates of the amount of surface water acidification.

Derivation of the site model

In the following derivation, we present only those equations used to calculate eventual (steady state) alkalinity and pH, two variables of primary interest in lake acidification. Calculations of eventual cation and sulphate concentrations are very similar to the alkalinity calculations. Throughout this derivation, wherever we have found it necessary to make an assumption about some process or parameter that is not strongly supported by existing evidence, we have erred on the conservative side (i.e. made the assumption that implies the minimum effect). Thus we argue below that acidification estimates derived from this model are probably minimum estimates.

The site model can be most simply represented as the equation:

$$(1)\quad [\mathrm{Alk}]_\infty = [\mathrm{Alk}]_o + \Delta[\mathrm{Alk}].$$

All the terms in this and subsequent equations are defined in Table 1. The derivation consists of three steps:

(1) Describing the change in alkalinity due to acidic deposition ($\Delta[\mathrm{Alk}]$), as a function of the assumed level of deposition, and estimated levels of acid neutralization within both the terrestrial watershed and the lake;
(2) Describing the lake's original alkalinity ($[\mathrm{Alk}]_o$) as a function of its current base cation, sulphate, and chloride concentrations (not alkalinity), and assumptions about how the lake's cations and sulphate have changed from original (preacidification) values; and
(3) Combining steps (1) and (2) in equation (1) to predict the eventual alkalinity ($[\mathrm{Alk}]_\infty$) resulting from a prespecified level of acidic deposition.

The model has no absolute time scale: $t=0$ represents the lake's expected condition in the absence of deposition of anthropogenic acids (i.e. all sulphate deposition that does occur is nonacidic, such as $CaSO_4$ dust particles); $t = t$ is the time during which lake chemistry samples (the primary input data) were taken; and $t = \infty$ describes the time when the watershed and lake are at steady state with respect to the assumed level of acidic deposition. If the lake's current chemistry is close to

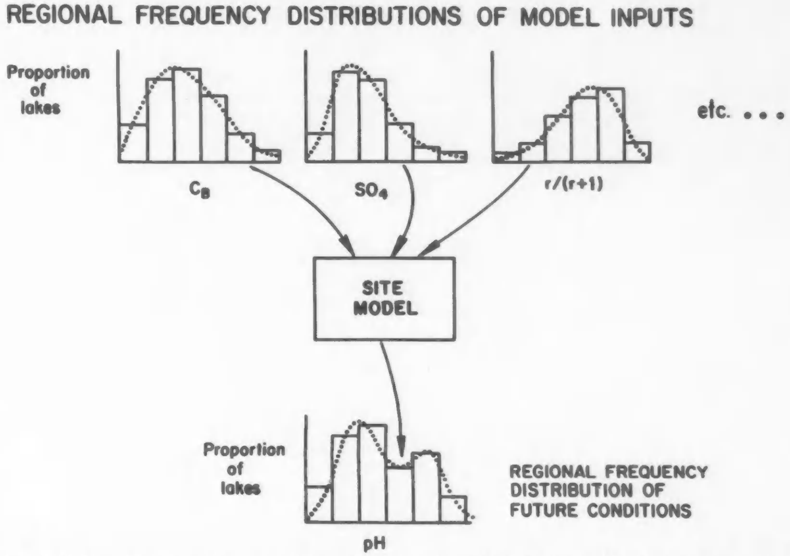
REGIONAL FREQUENCY DISTRIBUTIONS OF MODEL INPUTS
Proportion of lakes
C_B
SO_4
r/(r+1)
etc. . . .
SITE MODEL
Proportion of lakes
pH
REGIONAL FREQUENCY DISTRIBUTION OF FUTURE CONDITIONS

FIG. 1. A simplified conceptual overview of the regional model. The site model calculates the eventual pH of a single lake, given a set of input values. The regional model integrates over all observed combinations of input values for the lakes in a region, and generates a frequency distribution of eventual pH.

TABLE 1. Definitions of terms, units, and subscripts used in the model equations.

Variable	Description	Units
a,b	Parameters to calculate F_W	$\mu eq \cdot L^{-1}$
A	Area	m^2
Alk	Mean lake alkalinity	$\mu eq \cdot L^{-1}$
C_B	Total base cations	$\mu eq \cdot L^{-1}$
Cl	Lake chloride	$\mu eq \cdot L^{-1}$
D_a	Acidic sulphate deposition	$meq \cdot m^{-2} \cdot yr^{-1}$
D_n	Nonacidic sulphate deposition	$meq \cdot m^{-2} \cdot yr^{-1}$
F	Neutralization parameter	none
r	Watershed/lake area ratio	none
R	Runoff	$m \cdot yr^{-1}$
SO_4	Lake sulphate	$\mu eq \cdot L^{-1}$
S_s	Sulphate mass transfer coefficient	$m \cdot yr^{-1}$

Subscript	Meaning
W	Watershed
L	Lake
∞	Eventual
0	Original (zero acidic sulphate deposition)
t	Current

steady state with respect to deposition, then the predicted eventual alkalinity will be close to that which is currently observed.

Calculation of Δ Alkalinity

Lake water cation and alkalinity concentrations are affected by a complex combination of chemical and biological processes occurring in the lake and its watershed (NRCC 1981). Any model of acidification must include some representation of these processes. We chose to represent the level of neutralization of acidic sulphate deposition within the terrestrial watershed as the fraction of total deposition per unit area neutralized by weathering or cation exchange (F_W, a number between 0 and 1). This approach follows that used by Wright (1983) and others. We have deliberately left out of the model such parameters as soil depth and watershed slope, which are undoubtedly of importance in affecting neutralization processes (e.g. Chen et al. 1983), but were only known for a few intensively studied watersheds in eastern Canada. Within-lake neutralization of acidity (alkalinity generation) is assumed to occur as a consequence of sulphate reduction in the lake's sediments (Baker et al. 1986). The fraction of sulphate reaching the lake, both from direct deposition onto the lake and via the watershed, that is subsequently reduced is represented by F_L, also a number between 0 and 1. The deposited acidity that is not neutralized and therefore creates a change in lake alkalinity can be represented by:

$$(2)\quad \Delta[\mathrm{Alk}] = -\left[\frac{D_a\,(A_L+A_W)-D_a\cdot A_W\cdot F_W-D_a\cdot(A_L+A_W)\cdot F_L}{Q}\right].$$

Equation (2) explicitly recognizes the fact that all acidic sulphate deposited on the watershed can ultimately generate alkalinity through in-lake sulphate reduction, whether or not the H^+ accompanying the deposited sulphate is neutralized by soil cation exchange or other terrestrial watershed processes. Replacing Q by $(A_W+A_L)R$ (where R is the mean annual runoff (metres per year)) and then rearranging terms, one obtains:

$$(3a)\quad \Delta[\mathrm{Alk}] = -\frac{D_a}{R}\cdot\left[1-\frac{r}{r+1}F_W-F_L\right]$$

$$(3b)\quad \Delta[\mathrm{Alk}] = \begin{array}{ccc}\text{total acidic} & \text{watershed} & \text{lake}\\ \text{inputs} & \text{neutralization} & \text{neutralization.}\end{array}$$

The term $r/(r+1)$ is equivalent to $A_W/(A_W+A_L)$ where $r = A_W/A_L$. A very small proportion of watersheds (those with high levels of watershed and in-lake neutralization) can therefore experience a net alkalinization of their surface waters as a result of deposition of acidic sulphate. This is further discussed below.

Of the five variables in equation (3a), two are relatively easily obtained from existing data: R and r. Values of $[r/(r+1)]$ are in any case generally very close to 1 and do not greatly affect the predicted Δ[Alk]. Acidic sulphate deposition, D_a, can be either set as a control variable to simulate changes in deposition, or computed from measured wet sulphate deposition plus estimated dry sulphate deposition, minus nonacidic sulphate (contributed by sea-spray or deposited prairie dust). Nonacidic sulphate deposition (D_n) is calculated by assuming that its concentration is equal to that of base cations in wet deposition (Brydges and Summers 1989).

The value for F_W is assumed to be zero for lakes whose original cation concentration $[C_B]_0$ is less than some minimum value (a), and to increase linearly with $[C_B]_0$ up to a maximum value of one at some higher value (b). That is:

$$\begin{array}{lll} & F_W=0 & \text{for } [C_B]_0 \leqslant a \\ (4) & F_W=\dfrac{[C_B]_0-a}{b-a} & \text{for } a<[C_B]_0<b \\ & F_W=1 & \text{for } [C_B]_0 \geqslant b \end{array}$$

The rationale for assuming that F_W is related to $[C_B]_0$ is that the watershed properties which are considered responsible for low ionic strength surface waters, such as minimal soil contact time and low base supply rate (Schofield 1984), would also tend to reduce the proportion of acidity neutralized in the watershed (F_W). Put in other words, if in preindustrial times "clean rain" picked up few base cations as it passed through a given watershed (yielding low $[C_B]_0$), acid rain now falling on that watershed is less likely to be neutralized than that falling on a neighbouring watershed which has a higher $[C_B]_0$. Use of a constant F_W value greater than zero implies that a watershed's ability to at least partially neutralize deposited acidity can never be completely exhausted.

There are unfortunately very few data for confirming the assumed values for F_W, a, and b. Henriksen (1982) suggested that as acidic deposition increases, watershed cation export should increase (due to cation exchange in watershed soils), and that the change in lake base cation concentrations from the lake's original to its current condition should be proportional to the change in lake sulphate concentrations. He proposed an "*F*-factor," described by the ratio of the change in nonmarine calcium plus magnesium to the change in sulfate concentrations, or:

$$(5) \quad F = \frac{[\mathrm{Ca}^{2+}+\mathrm{Mg}^{2+}]_t-[\mathrm{Ca}^{2+}+\mathrm{Mg}^{2+}]_0}{[\mathrm{SO}_4{}^{-2}]_t-[\mathrm{SO}_4{}^{2-}]_0}$$

which has approximately the same effect functionally in his model (see Henriksen 1982; Wright 1983), as F_W does in ours. Henriksen (1982) estimated that F varied from 0.0 to 0.4 within sensitive Norwegian lakes, while time series data from Swan Lake in the Sudbury area of Ontario (where both sulphate and base cation concentrations have decreased) indicates that F may be as high as 0.64 (Dillon et al. 1986). Our assumption that F_W varies with $[C_B]_0$ is qualitatively consistent with the output of 140-yr simulations using a process-oriented model (Wright et al. 1986), which indicated that the Henriksen "*F*-factor" increased from 0.3 to 0.6, as original cation concentrations increased from 5 to 50 μeq·L^{-1}. Our method of estimating F_W is still simplistic, but it is more reasonable than the assumption of constant F_W across all watersheds.

The final parameter in equation (3a) is F_L. Here we assume that all in-lake alkalinity generation is due to sulphate reduction, and use the formulation developed by Kelly et al. (1987) and Baker et al. (1986) (recast in our notation) for estimating the proportion of sulphate retained:

$$(6) \quad F_L = \frac{S_s}{R\cdot(r+1)+S_s}$$

Kelly et al. (1987) point out that S_s (the sulphate mass transfer coefficient) can be thought of as "the height of the water column from which sulphate is removed each year" (e.g. 0.5 m). Across eastern Canada approximate ranges for R and r are 0.2–1.5 and 8–1000, so that with $S_s=0.5$, F_L can vary from essentially zero to a maximum of 0.25. Most F_L values are less than 0.1, however, so that only in a few watersheds (where F_W is close to 1 and runoff is low enough to yield significant values of F_L) does equation (3a) generate a positive value of Δ[Alk] as acidic sulphate deposition increases.

Substituting equations (4) and (6) into equation (3) yields an overall expression for the change in alkalinity due to acidic deposition:

$$(7) \quad \Delta\,[\mathrm{Alk}] = -\frac{D_a}{R}\left[1-\frac{r}{r+1}\cdot\left(\frac{[C_B]_0-a}{b-a}\right) - \frac{S_s}{R\cdot(r+1)+S_s}\right] \text{for } a<[C_B]_0<b.$$

Equations when $F_W=0$ or 1 are similar, but simpler.

Calculation of Original Alkalinity

Alkalinity is generally defined as the equivalent sum of all the bases that can be titrated with strong acid to a preselected equivalence point (Stumm and Morgan 1981), or:

$$(8) \quad [\mathrm{Alk}] = [\mathrm{HCO_3}] + [\mathrm{CO_3^{2-}}] + [\mathrm{OH^-}] + [\mathrm{RCOO^-}] - [\mathrm{H^+}],$$

where all concentrations are in equivalents and RCOO$^-$ refers to the set of organic anions present. An alternate equation, which is approximately equivalent to equation (9), can be derived by grouping together the remaining cations and anions (Driscoll et al. 1986):

$$(9) \quad [\mathrm{Alk}] = [C_B^{n+}] + [\mathrm{NH_4^+}] + [M^{n+}] - [\mathrm{SO_4^{2-}}] - [\mathrm{NO_3^-}] - [\mathrm{Cl^-}] - [\mathrm{F^{1-}}]$$

where M^{n+} represents metals (other than base cations) with various valences. This equation avoids the need to explicitly consider organic anion concentrations. We assume that in the absence of acidic conditions, the metals aluminum, iron, and manganese make negligible contributions to alkalinity. This assumption seems reasonable in light of the results of the U.S. E.P.A.'s Western Lake Survey of 719 lakes (Eilers et al. 1987), which found very low median concentrations of these metals in this low deposition region: extractable aluminum (0.31 μeq·L^{-1}), iron (0.73 μeq·L^{-1}, and manganese (0.03 μeq·L^{-1}). We further assume that the quantity ($[\mathrm{NH_4^+}] - [\mathrm{NO_3^-}] - [\mathrm{F^-}]$) is close to zero. Among the 474 lakes sampled in the U.S. EPA Eastern Lake Survey (Linthurst et al. 1986) which had alkalinities between 0 to 200 μeq·L^{-1}, ([NH$_4^+$] −

$[NO_3^-] - [F^-]$) averaged -2.47 μeq·L^{-1} ± 0.21 (SE). We then obtain the following expression for original alkalinity:

$$(10) \quad [Alk]_0 = [C_B]_0 - [Cl]_0 - [SO_4]_0$$

To calculate original alkalinity from equation (10) we need estimates of original cation, chloride, and sulphate concentrations. We assume no change in chloride levels due to acidification so that $[CL]_0 = [Cl]_t$. Original sulphate is calculated from non-acidic sulphate deposition (D_n), runoff, and within-lake sulphate reduction:

$$(11) \quad [SO_4]_0 = \frac{D_n}{R} \cdot [1 - Fv_L].$$

This approach assumes that watershed sources of sulphate are negligible, as suggested by Neary and Dillon (1988).

To estimate original cation concentrations, we follow the logic of Henriksen (1982) and estimate the change in cations from F_W and the change in sulphate:

$$(12) \quad [C_B]_0 = [C_B]_t - \frac{r}{r+1} F_W([SO_4]_t - [SO_4]_0)/(1 - F_L).$$

The $(1 - F_L)$ term corrects the change in sulphate for the influence of in-lake reduction on lake sulphate levels (the change in cations is due to a change in sulphate export from the watershed, not due to a change in lake sulphate levels). Since F_W is itself a function of $[C_B]_0$, we can replace F_W in equation (12) with equation (4):

$$(13) \quad [C_B]_0 = \frac{[C_B]_t + a\dfrac{r}{r+1}\left(\dfrac{[SO_4]_t - [SO_4]_0}{(b - a)\cdot(1 - F_L)}\right)}{1 + \dfrac{r}{r+1}\left(\dfrac{[SO_4]_t - [SO_4]_0}{(b - a)\cdot(1 - F_L)}\right)}.$$

Note that this procedure is not circular; it merely establishes quantitatively the link between $[C_B]_0$ and $([C_B]_t$, $(b - a)$, and $[SO_4]_t - [SO_4]_0)$, a link implicit in the definition of F_W. Since a and b are fixed and $(r/(r+1))$ varies little among lakes, it is lake to lake differences in the value of $([SO_4]_t - [SO_4]_0)/(1 - F_L)$ which drive the estimated regional variation in $[C_B]_t - [C_B]_0$. Variation in $[C_B]_t$ is of greater magnitude than that of $[SO_4]_t$, and therefore acts as the dominant control on estimated values of F_W.

Calculation of Eventual Alkalinity

We now have a basis for computing the value of each of the terms on the right hand side of equation (1). Substituting equations (7) and (10) into equation (1) yields an overall expression for eventual alkalinity:

$$(14) \quad [Alk]_\infty = [C_B]_0 - [Cl]_0 - [SO_4]_0 - \frac{D_a}{R} \cdot \left[1 - \frac{r}{r+1}\left(\frac{[C_B]_0 - a}{b - a}\right) - \frac{S_s}{R\cdot(r+1) + S_s}\right].$$

Calculation of pH from Alkalinity

The functional relationship between the alkalinity and pH of an aqueous solution can be described by equation (8) (Stumm and Morgan 1981). Given assumed values for the relevant dissociation constants, one can use numerical methods to solve this equation for the $[H^+]$ associated with any alkalinity. We used equation (8) to derive a titration curve for predicting pH from alkalinity, based on the assumptions that the contribution of organic anions (RCOO term) is negligible, and that $pCO_2 = 2.8$. The results of applying this titration curve to the National Inventory Survey (NIS) dataset (Kelso et al. 1986) and a subset of the U.S. EPA Eastern Lake Survey dataset (Linthurst et al. 1986) are presented in Fig. 2 and 3.

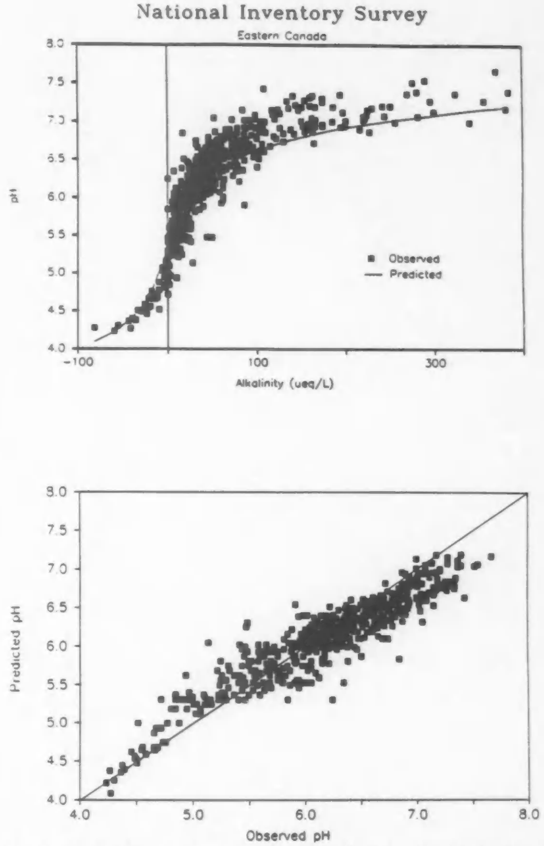

FIG. 2. Predicted and observed pH from alkalinity for the National Inventory Survey dataset ($n = 606$ lakes). Only lakes with alkalinities <400 μeq·L^{-1} were included.

The model fits the data quite well in both cases, suggesting that our assumptions regarding the importance of organic anions and the value of pCO_2 yield reasonable predictions. We justify the use of $pCO_2 = 2.8$ on the basis that: (1) the pH measurements used in this analysis were not derived from air-equilibrated solutions, so that one would expect pCO_2 to be less than 3.5); and (2) poorer fits were obtained when pCO_2 values of 2.5, 3.0, and 3.5 were tried. While there is some debate as to what the true value of pCO_2 is in surface waters (e.g. Herczeg and Hesslein 1984), our objective is to accurately predict the pH that would be measured in studies used to relate field pH to the presence or absence of species of biota. Thus reasonable prediction of the pH values reported from extensive lake surveys was our primary criterion for selection of a pCO_2 value. The method we are using tends to overestimate lake pH in the range below pH 5.0, so that acidification may be somewhat underestimated.

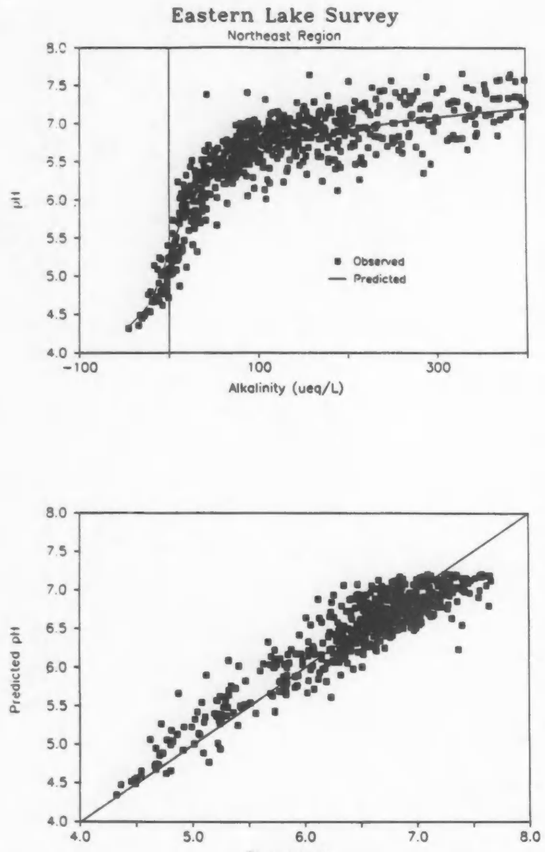

FIG. 3. Predicted and observed pH from alkalinity for the Eastern Lakes Survey, Northeast Regions data set ($n=653$ lakes). Only lakes with alkalinities <400 μeq·L^{-1} were included.

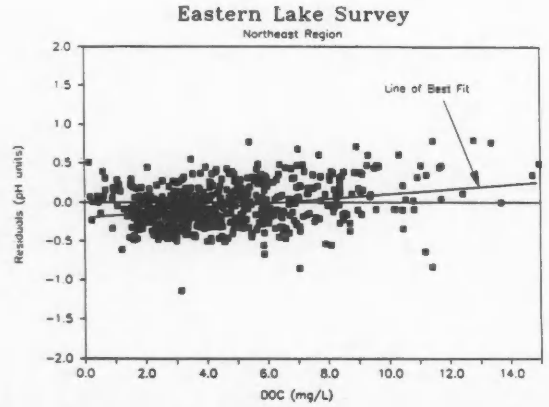

FIG. 4. Residuals (observed-predicted) from the theoretical titration curve from data from the Eastern Lake Survey, Northeast Region, plotted as a function of dissolved organic carbon (DOC).

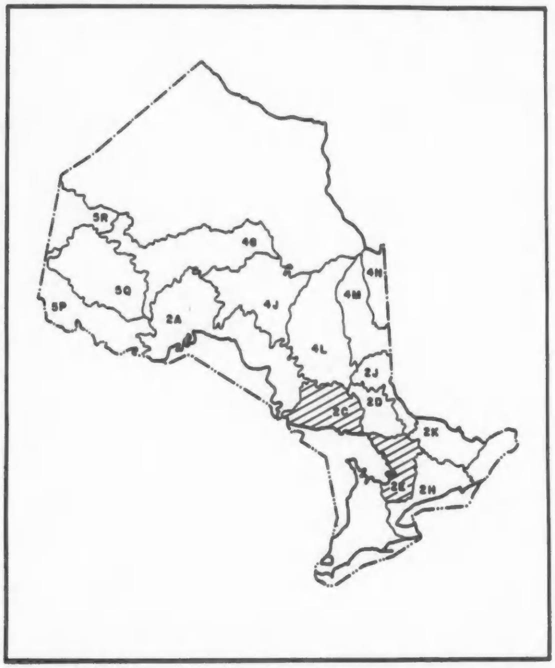

FIG. 5. Secondary watershed boundaries for regions of Ontario with acid-sensitive surface waters. The shaded areas are watersheds 2C and 2E, the areas used to illustrate application of the model, and for the sensitivity analysis.

Further evidence in support of ignoring organic anions in this regional analysis comes from an examination of the relationship between the residuals from our theoretical model and the observed dissolved organic carbon (DOC) of the lakes in the Eastern Lake Survey dataset (Fig. 4). The relationship, though statistically significant, is very weak ($r^2=0.116$). Better fits to the data were obtained using this approach (i.e. $p\mathrm{CO}_2=2.8$; $[\mathrm{RCOO}]=0$) than an earlier approach which used empirical estimates of [RCOO] based on DOC concentrations (described in Minns et al. 1986).

Application of the Model

Application of the site model for regional prediction is illustrated here using a secondary watershed in north-central Ontario (2C, Fig. 5). To apply the model to a region, one requires estimates of 10 model input variables ($[C_B]_t$, $[\mathrm{SO}_4]_t$, $[\mathrm{Cl}]_0$, r, R, D_a, $[\mathrm{SO}_4]_0$, a, b, and S_s) for all lakes in that region. It is clearly impractical to obtain these data directly for all lakes. We have assumed that survey data on water chemistry ($[C_B]_t$, $[\mathrm{SO}_4]_t$, hydrology (R), and lake and watershed sizes (r) are sufficient to describe the statistical distribution of these parameters among lakes in a region (Fig. 6). Because the Canadian survey data are not derived from random, or stratified random samples, there is some uncertainty as to whether they represent the true population of lakes in the region (Jones et al. 1990).

For the remaining six parameters, we have assumed that single values are representative of all lakes in the region. For D_a, we have obtained estimates of wet deposition from CAPMoN (Canadian Acidic Precipitation Monitoring Network) data for 1980, with dry deposition assumed to be a region-specific frac-

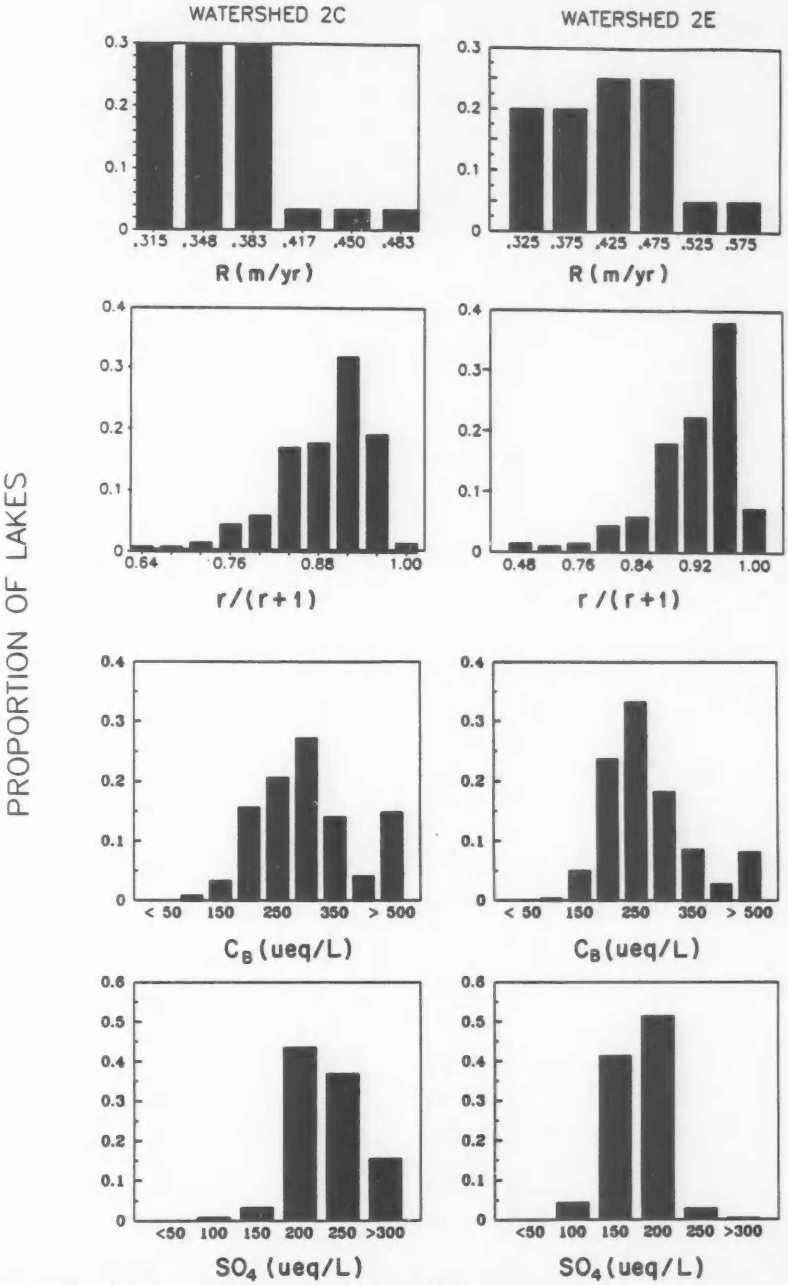

FIG. 6. Runoff, $r/(r+1)$, total cation, and sulphate distributions for Ontario watersheds 2C and 2E. Runoff distributions were derived from visual interpretation of runoff maps provided in the Hydrological Atlas of Canada. The distribution of $r/(r+1)$ was obtained from analyses of topographical maps of the area (Minns 1984). Cation and sulphate distributions were obtained using data from the Ontario Sensitivity Database (D. L. Wales, Ontario Ministry of Natural Resources, 99 Wellesley Street West, Toronto, Ontario., M7A 1W3, pers. comm.).

tion of wet, based on modelling estimates (P. Summers, Atmospheric Environment Service, 4905 Dufferin St., Downsview, Ont., M3H 5T4, pers. comm.). Original sulphate is calculated from D_n (Table 2), F_L, and runoff, using equation (11). Values for the remaining parameters were based on inferences from other studies of lake acidification.

TABLE 2. Parameter values used to apply the regional model to Ontario watersheds 2C and 2E.

	Assumed value		
Parameter	2C	2E	Source
S_s (μeq·L^{-1})	0.50	0.50	Kelly et al. (1987)
a,b (μeq·L^{-1})	0.,200.	0.,200.	see text on sensitivity analysis
D (kg/ha SO_4)			1980 CAPMoN data for wet and dry, 1985 CAPMoN data for nonacidic deposition (P. Summers, Atmospheric Environment Service, pers. comm.)
Wet (D_a)	26.70	33.96	
Dry (D_a)	12.60	20.21	
Nonacid (D_n)	6.69	7.47	
$[Cl]_0$	20.0	20.0	NIS data for Ontario (Kelso et al. 1986)

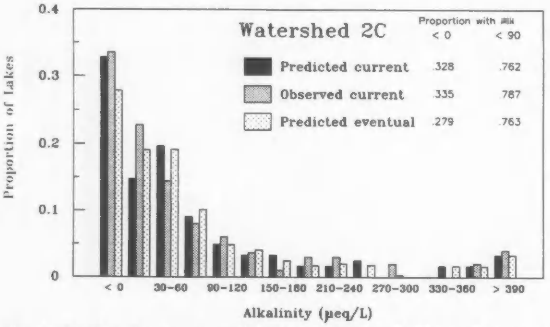

FIG. 7. Predicted current, predicted eventual, and observed current alkalinity distributions for Ontario watershed 2C. Also shown are the predicted and observed proportion of lakes in the area with alkalinities less than 0 to 90 μeq·L^{-1}.

The value chosen for b is particularly important, because it defines the upper threshold for acidification; a lake with $[C_B] \geqslant b$ is assigned a value of 1 for F_W, which implies an absence of watershed inputs of acidity, regardless of the level of acidic deposition (see equations (4) and (14)). We assumed that $b = 200$, a fairly conservative assumption (as discussed in "Sensitivity Analysis," below). We also conservatively assumed a minimal value for $a(=0)$, on the basis that lakes whose original cation concentrations approach zero would have had no watershed sources of bicarbonate or base cations to neutralize acidic deposition (i.e. $F_W = 0$). This assumption should hold in most lakes, except for those few lakes which originally had low alkalinity due to organic acidity, and watersheds with considerable sulphate retention capability. We discuss the issue of organic lakes in Jones et al. (1990). The measured value for $[C_B]_t$, together with assumed values for $[SO_4]_0$, a and b, are the primary determinants of $[C_B]_0$. Further details on the data and assumptions used to generate regional predictions are provided in the companion paper (Jones et al. 1990).

The regional model predicts the eventual alkalinity (Fig. 7) and pH distributions for all lakes in the region to which it is applied under the specified deposition stress. Because the predictions are of eventual conditions, in this case using the 1980 values of deposition, comparison with observed alkalinity distributions for the same region does not provide a test of the model. In Fig. 7, the predicted current alkalinity is also presented, as calculated from:

$$(15) \quad [Alk]_t = [C_B]_t - [Cl]_t - [SO_4]_t.$$

A comparison of the predicted and observed current alkalinity distributions is really only a test of the charge balance of the data from which both the current alkalinity and the cation and sulphate distributions were derived and of the assumptions that $[M]$, $[NH_4]$, $[NO_3]$, and $[F]$ together make a negligible net contribution to the charge balance. These assumptions were made for determining $[Alk]_0$ (equation (10)), and it is not critical to the success of the model that they apply under current conditions. Nevertheless, it is an interesting comparison to make because it indicates the effect of anions not included in equation (15). The predicted and observed distributions of current alkalinity (Fig. 7) are quite similar overall, and are virtually identical for the less-than-zero alkalinity category. In the next two alkalinity categories, the predicted alkalinity is less than observed (0–30 μeq·L^{-1} category) and greater than observed (30–60 μeq·L^{-1}).

The eventual alkalinity distribution is characterized by a smaller proportion of lakes in the less-than-zero alkalinity class (Fig. 7). The model thus predicts that under 1980 levels of sulphate deposition the majority of lakes in this area should recover somewhat from their current state. The modelled area includes lakes in the vicinity of Sudbury, Ontario (historically subject to very heavy local sources of deposition that have declined in the last decade); recent surveys have indicated significant increases in the alkalinity of lakes in this area (Keller and Pitblado 1986; Dillon et al. 1986). Thus the model is consistent with more recent observations, at least in this region.

Sensitivity Analysis

The site model contains two parameters whose values can only be inferred from data, rather than directly measured. These are original sulphate and F_W. The accuracy of our estimates of these parameters is thus difficult to judge, so it is useful to examine the sensitivity of the model's predictions to variations in their value over a range that is physically realistic. In this analysis we assume that the relationship between F_W and original cations (equation (4)) is true, that the parameter 'a' is equal to zero, and that our uncertainty lies exclusively with the value of the parameter 'b'.

The sensitivity of the site model to $[SO_4]_0$ can be shown by differentiating equation (14) with respect to $[SO_4]_0$, taking into account that $[C_B]_0$ is also a function of $[SO_4]_0$:

When $F_W = 0$, $[Alk]_\infty$ is inversely proportional to $[SO_4]_0$, simply reflecting the direct negative effect of $[SO_4]_0$ on $[Alk]_0$ (equation (10)). In this case $[C_B]_0 = [C_B]_t$. As $F_W/(1 - F_L)$

increases, the direct negative effect of $[SO_4]_0$ on $[Alk]_0$ is increasingly counteracted by the positive effect of $[SO_4]_0$ on $[C_B]_0$ (equation 12)). This means that the model's predictions will be most sensitive to $[SO_4]_0$ in acid sensitive lakes with low values of $[C_B]_t$ and F_W. Interestingly, this sensitivity diminishes as the model is exposed to more severe deposition scenarios (higher D_a/R), because the positive effect of $[SO_4]_0$ on $[C_B]_0$ results in less loss of alkalinity.

The combined sensitivity of the model to uncertainty in $[SO_4]_0$ and *b* is best illustrated by running the regional model while allowing both parameters to vary over a plausible range of values. Earlier investigations have indicated that plausible values of $[SO_4]_0$ range from approximately 10–100 $\mu eq \cdot L^{-1}$ (Wright 1983; Jones et al. 1984, 1987; Rogalla et al. 1986) depending on the assumptions underlying its derivation. As noted earlier, the *F*-value used by Henriksen and Wright has been estimated to vary from 0.0–0.7 in lakes considered sensitive to acidification. Since $(r/(r+1))$ is generally close to 0.9, and $F=(r/(r+1))F_W$, a similar range can be expected for F_W. Many previous investigators have considered 200 $\mu eq \cdot L^{-1}$ as a useful criterion for distinguishing lakes moderately sensitive to acidification from those that are less sensitive (reviewed by Linthurst et al. 1986). It is unlikely that lakes with original alkalinities less than 200 $\mu eq \cdot L^{-1}$ are insensitive to acidification; this suggests that a minumum plausible value for *b* would be 200. As an upper bound for this parameter we have chosen 1000. The latter value implies greater sensitivity for low alkalinity lakes ($F_W << 1$).

The sensitivity analysis was completed by running the regional model for Ontario watersheds 2C and 2E, using the distributions and parameters shown in Table 2 and Fig. 6, but allowing $[SO_4]_0$ to vary from 10–100 $\mu eq \cdot L^{-1}$ in increments of 10 and *b* to vary from 200–1000 $\mu eq \cdot L^{-1}$ in increments of 100. We have plotted the predicted proportion of acid lakes (eventual alkalinity less than zero), and the estimated average F_W value for the watershed for each combination of $[SO_4]_0$ and *b* (Fig. 8).

It is apparent from this figure that the predicted proportion of acid lakes is more sensitive to $[SO_4]_0$ than to *b*. In watershed 2C, the lakes are relatively close to steady state with respect to 1980 deposition levels. As expected the model shows relatively little sensitivity to *b* (or F_W) in this case. In contrast, the lakes in watershed 2E are relatively far from steady state, and the sensitivity to F_W is correspondingly greater.

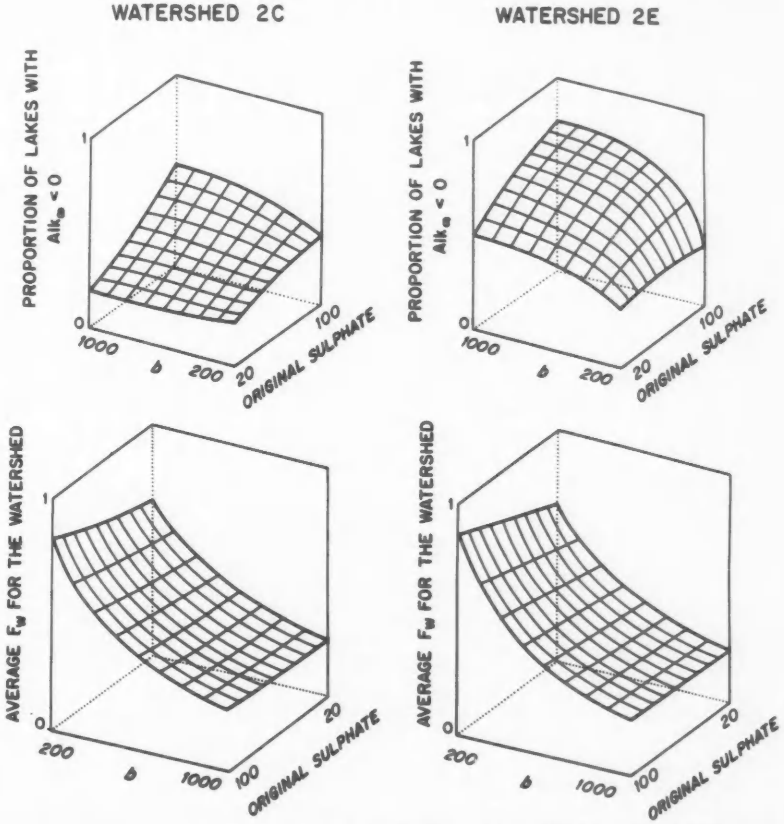

FIG. 8. The effect on model predictions of varying original sulphate ($[SO_4]_0$) and the '*b*' parameter of equation (4). Results are shown for watersheds 2C (includes the Sudbury area) and 2E (includes the Parry Sound-Muskoka-Haliburton area). The upper surfaces show the change in the proportion of acidic lakes (predicted eventual alkalinities <0); the lower surfaces show the change in the average regional value of F_W (computed from equation (4)). Note the differences in orientation of the upper and lower surfaces.

For both watersheds, the sensitivity to assumed values of $[SO_4]_0$ is considerable. Higher values of $[SO_4]_0$ reduce the estimates of the watershed's original alkalinity distribution ($[Alk]_0$), resulting in a greater extent of acidification for a given level of deposition. Finally, Fig. 8 clearly illustrates that in both watersheds the sensitivity of the model to $[SO_4]_0$ is greater for small values of F_W.

Discussion

Because the site model predicts eventual, steady state conditions, its overall predictions cannot be tested within a meaningful time frame. Many of the key model assumptions can be validated, however, either by examining regional datasets or by considering the results of intensive studies or experiments on single sites. Examples of the former have been provided here: (1) comparison of a theoretical pH–alkalinity relationship with Canadian and U.S. survey data; and (2) comparisons of predicted and observed current alkalinity distributions for watershed 2C. Results from more intensive studies have provided valuable information on the role of in-lake sulphate reduction as a source of alkalinity (Kelly et al. 1987; Baker et al. 1986). As evidence is obtained to validate or modify the model's assumptions, our confidence in the model's predictions will grow.

While the site model is closely related to the earlier models of Henriksen (1979, 1980); Thompson (1982); and Wright (1983), it contains some significant differences:

1. The site model accounts for differential cation exchange rates (as measured by *F*) in the lake itself and within its catchment. We explicitly assume cation exchange in the lake is negligible. Even though cation exchange reactions have been observed in lake sediments and may be an important buffering reserve (Oliver and Kelso 1982; Schindler et al. 1986), they are of greater quantitative importance after the lake has begun to acidify. Earlier authors have ignored this distinction, thereby implicitly assuming that the lake and its watershed have equivalent cation exchange rates.
2. The site model explicitly accounts for in-lake removal of sulphate, based on the model of Kelly et al. (1987); and Baker et al. (1986).
3. The site model treats both deposition and runoff as explicit input parameters, rather than simply using current (and expected future) lake sulphate concentrations as a measure of the net effect of these two parameters (Wright 1983). To the extent that in-lake (or in-catchment) removal of sulphate is significant, the approach used by Wright will yield incorrect results. The explicit treatment of deposition and runoff greatly facilitates the examination of alternative deposition scenarios (Jones et al. 1990). This was the primary purpose for the development of the regional model.

Our selection of a model which predicts the eventual steady state rather than one that predicts the changes in lake chemistry over time has both advantages and disadvantages. The primary disadvantage is that we are unable to say with any confidence whether the effects predicted will occur in 1 or 100 yr. The advantages include not having to specify: (1) an historical (or future) sequence of changes in acidic sulphate deposition; (2) a model of sulphate adsorption; (3) a reservoir of exchangeable base cations or (4) weathering rates. All four are necessary in the MAGIC model (Cosby et al. 1985), and the ILWAS model (Chen et al. 1983); the "enhanced Trickle-Down" model requires all of these components but the base cation reservoir (Schnoor et al. 1986). There are major uncertainties in estimating rates of sulphate adsorption and weathering from field data, due to the tremendous amount of spatial variation in soil composition within a watershed.

Our site model implicitly assumes a balanced input–output of sulphate which is most likely in eastern Canada (Rochelle and Church 1987). Weathering rates are implicitly tied to our assumptions about F_W. We have conservatively assumed that the exchangeable cation reservoirs in watersheds are inexhaustible, thereby minimizing our estimates of the ultimate extent of lake acidification. The MAGIC model assumes that the fraction of deposition neutralized decreases over time, as removal of cations by acidic deposition exceeds the rate of renewal of the cation pool by weathering.

The key uncertainties in the site model are the degree of watershed neutralization of acidic deposition (the F_W function: equation (4)), and the concentration of original sulphate ($[SO_4]_0$), which is linked directly to the determination of nonacidic sulphate deposition. F_W cannot be determined from survey data; instead intensive studies are required in which a large contrast in acidic deposition can be obtained and major ion input–output budgets carefully measured. Experimental manipulation of deposition levels, as implemented in the RAIN project (Wright et al. 1986) and planned for the U.S. EPA Watershed Manipulation Project (Thornton et al. 1986) are particularly valuable in this regard.

Original sulphate may not simply be derived through analysis of sulphate levels in remote areas, since background levels are strongly influenced by geographic and climatic factors. Improvements in estimates of $[SO_4]_0$ will require better estimates of the concentration of nonacidic sulphate in both wet and dry deposition. Both the spatial variability across subregions and the long term trend in nonacidic SO_4 deposition (due to road construction, land use changes, wind erosion on topsoil, etc.) need to be better understood.

The model presented in this paper provides a simple, and reasonably acceptable representation of our current understanding of the process of lake acidification and the major factors that govern this process. It might be argued that our present uncertainty with respect to some key parameters (especially F_W and $[SO_4]_0$ renders models of this type of limited value. The apparently large sensitivity of the model to this uncertainty (at least in $[SO_4]_0$) tempts one to question the significance of the results of applying the model on a local, let alone regional scale. Recognizing this potential criticism, we have been careful in both the development and application of the model to err on the conservative side, that is to underestimate rather than overestimate the potential damage from acid deposition. The assumptions which bias the model's predictions towards the conservative side include:

1. lakes with $[Alk]_0 > 200\ \mu eq \cdot L^{-1}$ cannot acidify ($F_W = 1$);
2. all lakes in a region have a limitless supply of exchangeable base cations;
3. only atmospheric deposition of nonacidic sulphate is considered in estimating original sulphate, (and not watershed sources of sulphate), leading to a potential underestimate of original sulphate and an overestimate of $[Alk]_0$,
4. the method we have used to compute lake pH from [Alk] tends to overestimate pH when pH<5.0;

(5) episodic pH depressions, which may have serious consequences for fisheries, are not considered; and

(6) atmospheric deposition of nitrate and ammonium is assumed to have no net acidifying effect.

Even with these conservative assumptions, the model's predicted effects on lakes in Eastern Canada is substantial and serious (Jones et al. 1990). In the long term, assumption (2) may lead to the most significant underestimates of acidification; for example Dillon et al. (1987) found that in Plastic Lake, base cation concentrations declined at about the same rate as ANC (about 2 $\mu eq \cdot L^{-1} \cdot yr^{-1}$), which they attributed to a decline in the watershed's pool of available cations. Assumption (3) may be somewhat counter-balanced by increases in atmospheric concentrations of nonacidic sulphate (e.g. dust, topsoil) due to land development since the preindustrial era. The model's assumption of constant nonacidic $[SO_4]$ in deposition thus may cause an overestimate of $[SO_4]_0$ in some areas.

Resolving the problem of acid deposition cannot wait for perfect knowledge. More complex existing models tend to simply disaggregate the uncertainty into many more, equally difficult to measure parameters such as rates of weathering and sulphate adsorption. Sensitivity analyses of these more complex models are also extremely difficult. Furthermore, they do not lend themselves to regional application without enormous efforts of field data collection. We maintain, therefore that models such as the one presented herein have a central role to play in the acid rain debate. Their predictions, and the assumptions upon which these predictions are based, should thus be carefully examined and improved where necessary, but not ignored.

Acknowledgements

Many scientists contributed to the early development of the model described in this paper. Their names are given in the Appendix. R. Hesslein, D. W. Schindler, G. T. Evans,and three anonymous reviewers provided numerous useful comments. Audrey Chui assisted with preparation of figures. The work was funded in part by contracts from Departments of Fisheries and Oceans Canada, Environment Canada, and a Federal Government Unsolicited Proposal Fund to ESSA Ltd.

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Assessing the Potential Extent of Damage to Inland Lakes in Eastern Canada due to Acidic Deposition: II. Application of the Regional Model[1]

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In this, the second of two papers on the development and application of a regional model of surface water acidification, we present the results of initial applications of the model to sensitive regions of eastern Canada. Data used for regional application of the model were obtained from a variety of sources, including acidic sulphate deposition monitoring data and regional lake water chemistry surveys. While these data do not provide a random sample of eastern Canadian lakes, we argue that there are no a priori reasons for expecting highly misleading biases in the data. Results of model applications are presented for observed 1980 sulphate deposition levels and for three alternative emission scenarios. The emission scenarios were simulated using a transfer matrix derived from the AES-LRTAP model. The results suggest that substantial additional damage (declines in surface water alkalinity and pH) is expected in some regions (e.g. northeastern Ontario), even at current deposition levels. The consequences of simple emission reduction strategies differ significantly among regions, suggesting that more complex strategies may be required to produce equitable benefits. To assist interpretation of a complex array of results, we propose an integrated representation of regional impacts that uses quantile-quantile plots of regional distributions of lake chemistry. Finally, we argue that while the results presented are highly uncertain, there are reasons to believe that, if anything, our damage estimates are conservative.

Cette seconde étude sur l'élaboration et l'application d'un modèle régional de l'acidification des eaux de surface présente les résultats de son application initiale à des régions sensibles de l'est du Canada. On a obtenu les données utilisées de diverses sources y compris des données sur le contrôle des précipitations de sulfate acide et des relevés régionaux des facteurs chimiques de lacs. Même si ces données ne constituent pas un échantillon aléatoire des lacs de l'est du Canada, les auteurs notent qu'il n'existe aucune raison a priori de s'attendre à des biais trompeurs dans les données. On présente les résultats de l'application du modèle au niveau observé en 1980 de précipitations de sulfate et de trois autres scénarios d'émission. Les scénarios d'émission ont été obtenus d'une matrice de passage dérivée du modèle AES-LRTAP. Les résultats portent à croire qu'on peut s'attendre à d'importants autres dommages (baisse de l'alcalinité et du pH des eaux de surface) dans certaines régions (par ex. nord-est de l'Ontario) même au niveau actuel de précipitations. Les conséquences d'une simple réduction des émissions varient nettement selon les régions, ce qui porte à croire que des stratégies plus complexes peuvent être nécessaires pour donner des avantages équitables. Afin d'aider à l'interprétation d'un groupe complexe de résultats, on propose une représentation intégrée des incidences régionales à l'aide de graphiques quantile-quantile de la répartition régionale des caractéristiques chimiques lacustres. En dernier lieu, on soutient que même si les résultats présentés sont très aléatoires, il y a raison de croire que les estimations des dommages ne sont rien moins que prudentes.

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Acidic deposition and its impact on aquatic resources continues to be one of the most prominent environmental issues in North America and Europe. In recent years, much of the interest in this issue has focused on the regional (provincial, national) extent of the problem. Large scale aquatic surveys have documented the areas of North America containing lakes sensitive to acidic deposition (Jeffries et al. 1986; Kelso et al. 1986; Linthurst et al. 1986), and have provided some evidence of the magnitude of impacts that have already occurred. In addition to surveys of the current extent of effects, models are needed that allow credible prediction of the consequences of control measures (or the lack thereof) to the aquatic resources at risk. Due to the extensive nature of this problem, to date only relatively simple models have been used, since the more complex, mechanistic models (e.g. Christopherson and Wright 1981; Chen et al. 1983; Cosby et al. 1985) have very significant input and calibration requirements. The United States Environmental Protection Agency (U.S. EPA) Direct-Delayed Response Project is attempting to use three mechanistic models to make regional predictions by calibrating these models to data from about 150 watersheds that are a stratified random sample of the regional lake population. Simple regional models have been developed and applied to surface waters in the United States (Small and Sutton 1986; Rogalla et al. 1986; Schindler et al. 1989) and northern Europe (Alcamo et al. 1987) but, to date, equivalent models for Canadian lakes do not exist.

TABLE 1. Definitions of terms, units, and subscripts used in the model equations.

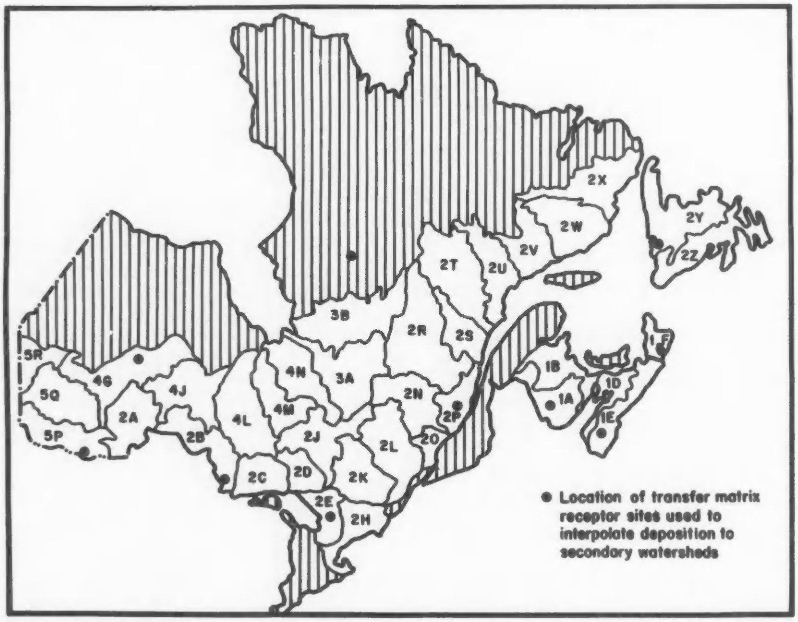
Variable	Description	Units
a,b	Parameters to calculate F_W	$\mu eq \cdot L^{-1}$
Alk	Mean lake alkalinity	$\mu eq \cdot L^{-1}$
C_B	Total base cations	$\mu eq \cdot L^{-1}$
Cl	Lake chloride	$\mu eq \cdot L^{-1}$
D_a	Acidic sulphate deposition	$meq \cdot m^{-2} \cdot yr^{-1}$
D_n	Nonacidic sulphate deposition	$meq \cdot m^{-2} \cdot yr^{-1}$
F	Neutralization parameter	None
r	Watershed/lake area ratio	None
R	Runoff	$m \cdot yr^{-1}$
SO_4	Lake sulphate	$\mu eq \cdot L^{-1}$
S_s	Sulphate mass transfer coefficient	$m \cdot yr^{-1}$

Subscript	Meaning
W	Watershed
L	Lake
∞	Eventual
0	Original (zero acidic sulphate deposition)
t	Current

In a companion paper (Marmorek et al. 1990), we derived and examined a simple acidification model (the "site" model), developed specifically to allow regional impact prediction. In this paper, we apply the model to sensitive areas of eastern Canada receiving significantly elevated acidic sulphate deposition rates, and examine the consequences of two proposed emission control strategies.

Assumptions and Data Sources

The site model is based on the earlier models of Henriksen (1979, 1980); Thompson (1982); and Wright (1983). The model predicts the expected eventual alkalinity for an individual lake,


2X
2W
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2U
3B
2R
2S
5R
4G
1F
1B
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4J
4N
3A
1D
2A
4M
2N
1A
4L
2P
1E
5P
2B
2J
2O
2L
2C
2D
2K
2E
2H
● Location of transfer matrix receptor sites used to interpolate deposition to secondary watersheds

FIG. 1. Secondary watersheds included in the regional model. The shaded areas were excluded from our analysis either due to the absence of sensitive lakes or their remoteness from sources of acidic deposition. Also shown (closed circles) are the nine receptor sites used, together with the source–receptor matrix of Olson et al. (1983), to estimate changes in acidic sulphate deposition to each secondary watershed as a consequence of a given emission control strategy.

TABLE 2. Sources of data used to describe current chemistry ($[C_0]_t$, $[SO_4]_t$), runoff and ($r/(r+1)$) distributions for each secondary watershed of interest in eastern Canada.

1. $[C_B]_t$, $[SO_4]_t$
   - Ontario: Ontario Sensitivity Database, D. L. Wales, Ontario Ministry of Natural Resources, 99 Wellesley St. West, Toronto, Ont., M7A 1W3, pers. comm.)
   - Quebec: Extracted from Naquadat Database, A. Fraser, Environment Canada, P.O. Box 5050, Burlington, Ont. pers. comm.).
   - Nova Scotia and New Brunswick: National Inventory Survey, Kelso et al. (1986).
   - Newfoundland: Newfoundland Lake Survey, Scruton (1984)
2. $r/(r+1)$
   - Ontario: Counts and Measures data from Minns (1984)
   - Other Provinces: Unpubl. data
3. Runoff
   - All provinces: Visually interpreted from isolines in the Hydrological Atlas of Canada (Surveys and Mapping Branch, Department of Energy, Mines, and Resources. Ottawa. 1978. 34 maps.)

TABLE 3. Sample sizes (number of lakes) and secondary watershed substitutions (where required) for $r/(r+1)$ and current lake chemistry data for Ontario, Quebec, and the Maritime provinces. For watersheds where required, the source watershed for the substitution is shown in parentheses. For several secondary watersheds in Quebec, adequate sample sizes were achieved by lumping data from adjacent watersheds rather than by substitution.

Secondary watershed	$r/(r+1)$	Current lake chemistry (C_B, SO_4)
Ontario		
2A	209	63
2B	412	221
2C	136	122
2D	171	108
2E	205	538
2H	144	108
2J	436	141
2K	138	425
4G	214	172 (4J)
4J	237	172
4L	53	223
4M	147 (4N)	223 (4L)
4N	147	223 (4L)
5P	73	246
5Q	180	46
5R	259	46 (5Q)
Quebec		
2J	215 (2K)	41 (2J+2K)
2K	215	41 (2J+2K)
2L	215 (2K)	166
2N	311 (2O)	40
2O	311	33
2P	311 (2O)	50
2R	220	72
2S	355 (2U)	79 (2S+2T+2U)
2T	355 (2U)	79 (2S+2T+2U)
2U	355	79 (2S+2T+2U)
2V	355 (2U)	42
2W	355 (2U)	(2V+2W+2X)
2X	355 (2U)	42
3A	220 (2R)	(2V+2W+2X)
3B	220 (2R)	42
		(2V+2W+2X)
		72 (2R)
		72 (2R)
Maritimes		
1A	706	69 (1A+1B)
1B	365	69 (1A+1B)
1D	365	41
1E	1879	34
1F	203	41 (1D)
2Y	3876	255
2Z	3876 (2Y)	32

based on estimates of the lake's original alkalinity and the change in alkalinity due to acidic sulphate deposition. From Marmorek et al. (1990), the complete site model for alkalinity is described by (symbols defined in Table 1).

$$(1)\quad [\mathrm{Alk}]_\infty = [\mathrm{Alk}]_0 + \Delta[\mathrm{Alk}]$$

$$(2)\quad [\mathrm{Alk}]_0 = [C_B]_0 - [\mathrm{Cl}]_0 - [\mathrm{SO}_4]_0$$

$$(3)\quad \Delta[\mathrm{Alk}] = \frac{D_a}{R}\left[1 - \frac{r}{r+1}F_W - F_L\right]$$

$$(4)\quad [C_B]_0 = [C_B]_t - \frac{r}{r+1}F_W\,DSO_4$$

$$(5)\quad \begin{cases} F_W = 0. & \text{, for } [C_B]_0 < a \\ F_W = \dfrac{[C_B]_0 - a}{(b-a)} & \text{, for } a \leqslant [C_B]_0 < b \\ F_W = 1. & \text{, for } [C_B]_0 \geqslant b \end{cases}$$

$$(6)\quad F_L = \frac{S_s}{R(r+1) + S_s}$$

$$(7)\quad DSO_4 = ([\mathrm{SO}_4]_t - [\mathrm{SO}_4]_0)\,/\,(1 - F_L)$$

Eventual pH is calculated from alkalinity using an empirical titration curve that closely fits observed pH–alkalinity data from extensive lake surveys.

To apply the model regionally, we need to estimate the original alkalinity distribution for the lakes in a region, as well as the distributions of other site model parameters that influence the change in alkalinity and that are expected to vary among lakes. We assume that $[\mathrm{C1}]_0$, $[\mathrm{SO}_4]_0$, the pH–alkalinity titration curve, S_s, and the relationship between F_w and original cations are constant for all lakes in a region. Site model parameters for which distributions are required are thus $[C_B]_t$ $[\mathrm{SO}_4]_t$, R, D_a, and ($r/(r+1)$).

The overall region of concern was defined as the area of Canada east of the Ontario–Manitoba border and south of latitude 52°N (Fig. 1). The northern boundary was selected to exclude zones with wet sulphate deposition less than 10 kg $\mathrm{SO}_4 \cdot \mathrm{ha}^{-1}$ (based on 1980 Canadian Acidic Precipitation Monitoring Network (CAPMoN) wet sulphate deposition data). Within this overall area, three other regions were excluded due to the high neutralization capacity of their soils: southwestern Ontario, the St. Lawrence valley in Quebec, including the Gaspé Peninsula, and Anticosti Island, and Prince Edward Island.

One of the important questions that the regional model should be able to address is whether the benefits of emission controls are distributed uniformly throughout eastern Canada. This

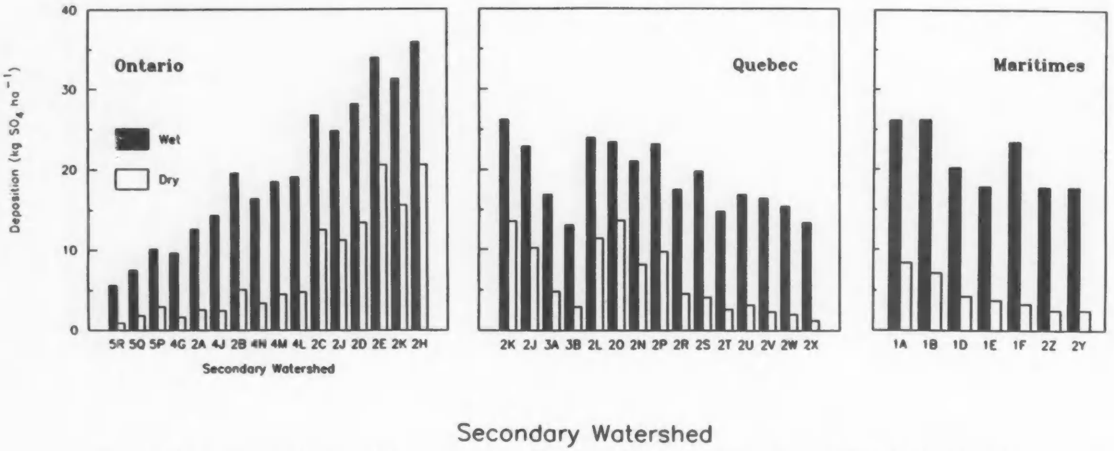

FIG. 2. Observed wet and estimated dry sulphur deposition rates for the secondary watersheds included in this study.

requires that the model be able to make specific predictions of eventual alkalinity and pH distributions for subregions within eastern Canada. We have chosen secondary watersheds (Fig. 1) as our spatial unit for regional prediction, of which there are 38 in area defined above. Within a secondary watershed, we assume that deposition rates will be spatially uniform.

The sources of data used to describe the current cations and sulphate, runoff, and ($r/(r + 1)$) distributions for each secondary watershed are presented in Table 2. To use the water chemistry survey data to estimate original alkalinities, we require estimates of $[SO_4]_0$ and F_w. As noted in the earlier paper (Marmorek et al. 1990), there are no generally accepted estimates of these parameters. Furthermore, the model is sensitive to estimates of both.

To obtain estimates of $[SO_4]_0$ for each secondary watershed, we have assumed that local, terrestrial sources of nonacidic sulphate are negligible and, therefore, that nonacidic sulphate deposition is the principal source of original lake $[SO_4]_0$ (Neary and Dillon 1988). Nonacidic sulphate deposition is estimated from base cation concentrations in deposition (Brydges and Summers 1989) and $[SO_4]_o$ is then calculated from:

$$(8) \quad [SO_4]_0 = \frac{D_n}{R}[1 - F_L].$$

This is likely to yield a minimum estimate of $[SO_4]_0$; underestimates of $[SO_4]_0$ will lead to underestimates of the effects of acidic deposition.

In the companion paper, we argued that a reasonable range for the b parameter of the $F_w - [C_B]_0$ relationship was 200–1000 $\mu eq \cdot L^{-1}$. For two secondary watersheds in north-central Ontario, this translated into average F_w values for the surveyed lakes in these regions ranging approximately from 0.8 down to 0.2 (the average value of F_w varies inversely with b). These values are within the range of F values cited elsewhere (Henriksen 1982; Johnson et al. 1985; Dillon et al. 1986; Wright et al. 1986). To be consistent with our conservative assumption for the value of $[SO_4]_0$, we have assumed for the analyses presented herein that $b = 200$ $\mu eq \cdot L^{-1}$, which implies a relatively high value for F_w, on average (approximately 0.6 for north-central Ontario lakes). The larger the value of F_w, the less the effect (on lake acidity) of increased (or decreased) acidic sulphate deposition.

For several secondary watersheds, the data necessary to characterize original alkalinity or $r(r+1)$ distributions were either insufficient or unavailable. In these instances, we have substituted data from nearby watersheds or lumped data from more than one watershed (Table 3). Few data substitutions were necessary in the Maritimes. Within Ontario, those watersheds with data substitutions are all in parts of the province receiving low levels of acidic deposition, so this procedure is unlikely to significantly affect damage estimates. In Quebec, however, data substitutions make a substantial contribution to the uncertainty in predictions.

Chloride data were not available for most surveyed lakes in Ontario and Quebec. For all secondary watersheds in Ontario and Quebec, therefore, we assumed a single value of $[Cl]_0$ (20 and 13 $\mu eq \cdot L^{-1}$, respectively) in calculating $[Alk]_0$ distributions. These values were derived from an analysis of the National Inventory Survey database (Kelso et al. 1986). In areas remote from marine salt influences, chloride levels do not vary greatly, except where road salt contributions are significant. Instances of the latter were felt to be sufficiently uncommon in the data bases used to establish $[Alk]_0$ distributions to allow them to be ignored. Average [Cl] in the 179 and 250 inland lakes sampled for the NIS in Ontario and Quebec, respectively, were only 19.07 and 12.65. No lakes sampled in Quebec and only two lakes in Ontario had [Cl] values greater than 40 $\mu eq \cdot L^{-1}$.

To apply the distributions to the site model, we divided the $[Alk]_0$, R and $r/(r+1)$ distributions into a number (6–15) of discrete classes, with a frequency (proportion of lakes in the region) associated with each class. Together with values for D_a, S_s, a, and b, each unique combination of $[Alk]_0$, R, and $r/(r+1)$ classes can be applied to the site model to estimate an eventual alkalinity (and pH) for that "lake type." By assuming that the three distributions are independent, the proportion of lakes of a given type is simply:

$$(9) \qquad P_{i,j,k} = P_i \cdot P_j \cdot P_k$$

where P_i = proportion of lakes in $[Alk]_0$ class i; P_j = proportion of lakes in R class j; P_k = proportion of lakes in $r/(r+1)$ class k.

The calculation of eventual alkalinity can be repeated for all lake types, and eventual alkalinity and pH distributions gen-

TABLE 4. Estimated original, current, and eventual median alkalinity and pH values for secondary watersheds, and regional summaries. Eventual predictions are based on 1980 deposition levels.

Region	Median alkalinity			Median pH		
	Original	Current	Eventual	Original	Current	Eventual
Total	91	72	70	6.57	6.46	6.44
Ontario	295	302	300	7.09	7.09	7.09
2A	367	375	374	7.18	7.18	7.18
2B	249	249	250	7.01	7.01	7.01
2C	83	34	35	6.50	6.13	6.16
2D	87	44	31	6.55	6.27	6.11
2E	86	53	26	6.54	6.33	6.03
2H	150	150	161	6.79	6.80	6.81
2J	122	104	99	6.69	6.62	6.61
2K	103	95	81	6.61	6.59	6.50
4G	>390	>390	>390	>7.60	>7.60	>7.60
4J	>390	>390	>390	>7.60	>7.60	>7.60
4L	>390	>390	>390	7.59	7.59	7.59
4M	>390	>390	>390	7.59	7.59	7.59
4N	>390	>390	>390	7.59	7.59	7.59
5P	216	220	222	6.93	6.94	6.95
5Q	276	288	284	7.07	7.08	7.08
5R	267	288	284	7.07	7.08	7.08
Quebec	86	65	58	6.54	6.41	6.37
2J	117	83	84	6.69	6.54	6.53
2K	114	83	97	6.66	6.54	6.56
2L	154	150	150	6.80	6.79	6.79
2N	84	55	49	6.55	6.35	6.26
2O	148	145	144	6.79	6.75	6.76
2P	95	53	53	6.56	6.32	6.32
2R	108	84	86	6.65	6.54	6.53
2S	77	56	47	6.46	6.35	6.27
2T	80	56	56	6.50	6.35	6.35
2U	80	56	54	6.49	6.35	6.34
2V	59	48	32	6.39	6.27	6.16
2W	59	48	34	6.39	6.27	6.19
2X	58	48	37	6.39	6.27	6.20
3A	108	84	82	6.65	6.54	6.52
3B	108	84	90	6.65	6.54	6.54
Maritimes	75	53	55	6.47	6.46	6.44
1A	89	52	40	6.54	6.33	6.23
1B	91	52	56	6.55	6.33	6.34
1D[a]	53	12	20	6.33	5.65	5.93
1E[a]	26	<0	1	6.06	4.65	5.33
1F[a]	53	12	24	6.33	5.65	6.05
2Y	91	78	76	6.55	6.50	6.48
2Z	60	38	44	6.37	6.18	6.23

[a] For secondary watershed calculations, Nova Scotia lakes include only those on weathering-resistant bedrock; for regional summaries all lakes are included.

erated for the region by weighting each calculated eventual alkalinity according to the $P_{i,j,k}$ for that lake type.

As mentioned above, this approach relies upon the assumption that the distributions of $[\mathrm{Alk}]_0$, R and $r/(r+1)$ are statistically independent of each other. Because our distributions for these three parameters were derived from different sources, it is not possible for us to test this assumption directly. Certainly on a broad regional scale, cation concentrations (and thus Alk_0) increase from east to west (Kelso et al. 1986; Jeffries et al. 1986), while runoff tends to decrease, thus suggesting a lack of independence. By specifying different, independent distributions for each secondary watershed, we expect to have accounted for such large scale biases, however. We are, nevertheless, required to assume that correlations among parameters on the more local, secondary watershed scale are not significant.

A second critical assumption, implied by using survey data to estimate the regional impacts of acidic deposition, is that the surveys provide a representative sample of the population of lakes in the region. Unfortunately, this is not strictly speaking the case for existing surveys of Canadian surface waters. In Ontario, our database is biased towards relatively large lakes containing game fish populations. In Nova Scotia, the data were principally collected from lakes in areas particularly sensitive to acidification. In other provinces, we have no reason to believe that the survey data, upon which this analysis is based, are biased towards a particular subset of the overall set of lakes in the region being surveyed.

The Ontario dataset is, if anything, biased towards less sensitive lakes; thus we will tend to underestimate impacts in this

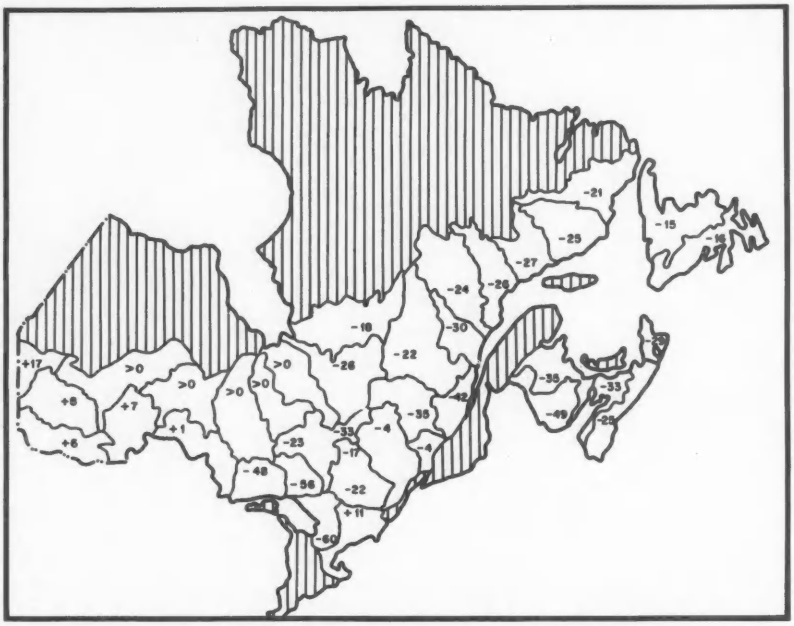

FIG. 3. Predicted changes in median lake alkalinities ($\mu eq \cdot L^{-1}$) for secondary watersheds in eastern Canada, from original to eventual conditions assuming 1980 deposition rates. Two values are presented for watersheds 2J and 2K, one each for the Quebec and Ontario portions of these watersheds.

province. We have not attempted to correct this bias since there is no objective means of doing so, and ignoring the bias is consistent with the conservative nature of other assumptions we have used (Marmorek et al. 1990). To avoid overestimating the regional scale damage in Nova Scotia, we assume that the surveyed lakes only represent lakes in catchments with predominantly noncarbonate bearing, weathering-resistant bedrock, and that the remaining lakes in the region are unaffected by acidification.

To simulate the consequences of a proposed emission control strategy, we required a means of translating changes in emissions into changes in deposition patterns. This was accomplished using a source-receptor transfer matrix described by Olson et al. (1983). The transfer matrix contains 360 entries, representing the predicted transport of sulphur emissions from 40 source regions throughout North America to deposition at nine Canadian receptor sites (Fig. 1). The matrix entries are derived from wet sulphur deposition predictions using the AES-LRTAP model (Olson et al. 1983). Dry deposition is assumed to be a region-specific fraction of predicted wet deposition, based on a comparison of modelled dry deposition estimates for 1980 (P. Summers, Atmospheric Environment Service, 4905 Dufferin St., Downsview, Ont. M3H 5T4, pers. comm.) to observed 1980 wet deposition (Fig. 2).

The AES-LRTAP model is but one of several source-receptor models that have been used to develop sulphur transfer matrices (Ferguson and Machta 1982). Presently, there is no consensus on whch of these models is the "best" one, due to the great difficulty in validating their predictions. We have arbitrarily selected the AES-LRTAP model to illustrate our approach to regional assessment of the effects of emission controls; a more comprehensive assessment should consider the variability introduced by using transfer matrices derived from more than one atmospheric model (Ellis 1988).

To interpolate from the nine receptor sites to the 38 secondary watersheds, we estimated the expected deposition at the approximate centroid of each watershed using an inverse-square distance weighting algorithm (Patterson et al. 1981):

$$(10) \quad Dw_i = \sum_j Dr_j \cdot (1/d_{i,j}^2) \Big/ \left(\sum_j (1/d_{i,j}^2) \right)$$

where d_{ij} = the distance between the centroid of watershed (i) and receptor site (j); Dw_i = estimated deposition at watershed (i); and Dr_j = estimated deposition at receptor site (j). Given the wide distribution of the nine receptor sites (Fig. 1), we feel this interpolation method provides sufficient accuracy for our purposes here.

We ran the regional model for all 38 secondary watersheds, using the data and assumptions described above. The model generates distributions of original, current, and eventual pH and alkalinity for each watershed by sulphate deposition scenario. In addition to original and eventual alkalinity (equations (2) and (1), respectively), we calculate current alkalinity using the equation.

$$(11) \quad [\mathrm{Alk}]_t = [C_B]_t - [\mathrm{Cl}]_t - [\mathrm{SO_4}]_t.$$

This estimate of current alkalinity is derived from the principle of charge balance, and by assuming that concentrations of other cations and anions (NO_3, NH_4, F, A1, H^+, organic anions) are negligible. The estimates of $[\mathrm{Alk}]_t$ will be underestimates in acidic lakes (high concentrations of H^+, Al) and overestimates in coloured waters (high concentrations of organic anions). Note that observed current lake sulphate levels, $[\mathrm{SO_4}]_t$, were used rather than the values predicted from sulphate deposition.

TABLE 5. Estimated 1980 sulphur dioxide emissions for 15 source regions in Canada and 25 in the United States, as calculated by Work Group 2 of the U.S.–Canada Memorandum of Intent (Ferguson and Machta 1982). These figures were used in the 1980 baseline scenario, and used to derive the three additional control scenarios. See text for further explanation of scenarios.

Canada		United States	
Region[a]	Emissions (KT SO_2)	Region	Emissions (KT SO_2)
NMN	699.13	OHO	2401.1
SMN	38.87	ILL	1334.1
NWO	29.77	PENN	1834.5
NEO	215.94	IND	1821.5
SUD	1126.39	KEN	1016.7
SWO	779.93	MCH	822.7
SEO	41.95	TENN	976.6
SLV	437.81	MSU	1180.4
NQU	524.51	WVR	986.8
GBY	122.67	NYK	856.7
NBK	215.00	ALA	688.3
NSP	225.00	WIO	876.4
NFL	59.00	MIN	236.2
ASK	597.15	VNC	873.9
BCA	192.87	FLD	993.3
Total	5305.99	GSC	1057.5
		MDJ	672.5
		ALM	626.6
		MCR	391.5
		MAN	86.0
		VNH	90.5
		WNE	515.7
		WSE	1832.6
		WNW	343.7
		WSW	1506.7
		Total	24022.5

[a] For an explanation of the source region identifier codes see Ferguson and Machta (1982).

As with an earlier version of the regional model (Jones et al. 1984), our estimates of regional scale impacts are summarized as the proportions of the total numbers of lakes in a secondary watershed, province, or in eastern Canada, that will lie in a given pH or alkalinity interval. The results to not apply to the area of lakes affected, since lake sensitivity and lake size are not independent of one another (i.e. there are disproportionately few highly sensitive, large lakes).

Further details on the data and assumptions used in this analysis can be found in Jones et al. (1987).

Results

Regional Changes in Lake Chemistry

The predicted magnitude of chemical changes expected for acidic sulphate deposition rates equivalent to those measured in 1980 (baseline scenario) can be seen by considering median alkalinity and pH values. The model predicts considerable changes in median alkalinity and pH for virtually all regions where median original alkalinities are less than 150 $\mu eq \cdot L^{-1}$ (Table 4; Fig. 3). Also, significant additional decreases from current levels are expected in several watersheds.

The changes are greatest in northeastern Ontario (Fig. 3.). Decreases of 20–60 $\mu eq \cdot L^{-1}$ from original to eventual median alkalinity are predicted for these watersheds (pH declines of 0.1–0.5 units). In Quebec, alkalinity declines range from 4–42 $\mu eq \cdot L^{-1}$, while in the Maritimes, the range is 15–49 $\mu eq \cdot L^{-1}$.

In regions with median alkalinities >150 $\mu eq \cdot L^{-1}$, the response to increased acidic sulphate deposition appears to be an increase in median alkalinity. This counter-intuitive result is actually the expected consequence of the combined effect of a high value of F_W and in-lake sulphur reduction processes. The high value of F_W implies that most, if not all, of the sulphate reaching the lake from the watershed is already neutralized (i.e. through watershed cation exchange). Having reached the lake, some of this sulphate is then reduced in the sediments (the F_L term in equation (2)), thereby generating sufficient additional alkalinity to more than cancel out the added acidity from direct deposition to the lake.

The overall magnitude of alkalinity change (from original to predicted eventual) in Ontario is actually positive (+5 $\mu eq \cdot L^{-1}$), due to the large number of remote, high alkalinity lakes in the Ontario watersheds in regions 4 and 5, and on the north shore of Lake Superior exhibiting the effect described above. In contrast, relatively large negative changes (28 $\mu eq \cdot L^{-1}$) are expected on the provincial scale in Quebec, which has a large area south of 52°N latitude containing soils and bedrock with a low potential to neutralize acidic inputs (Shilts 1981). In the Maritimes, the predicted decrease is somewhat less (20 $\mu eq \cdot L^{-1}$); it is noteworthy that in several secondary watersheds in the Maritimes, some recovery is predicted from current values, given a continuation of 1980 deposition rates.

Overall, the median alkalinity in the 38 secondary watersheds is predicted to decline from an original level of 91 $\mu eq \cdot L^{-1}$ to an eventual level of 70 at 1980 deposition levels. The eventual level is less than the estimated current value of 72, indicating that, overall, further acidification is expected at 1980 deposition rates. This additional decline is explained by differences between observed current lake (1982–84) sulphate concentrations and those concentrations predicted from total acidic sulphate deposition adjusted for evaporative concentration and in-lake reduction.

The largest additional alkalinity decline (current to eventual) is predicted to occur in watershed 2E (27 $\mu eq \cdot L^{-1}$). Fifty percent of the lakes in watershed 2E are predicted to eventually reach an alkalinity of 26 $\mu eq \cdot L^{-1}$ or less (i.e. 2173) lakes. This secondary watershed includes Plastic Lake, the only intensively monitored lake in North America shown to be currently losing alkalinity (Dillon et al. 1987).

Expected Effects of Emission Controls

The results above indicate that, in most regions with large numbers of lakes sensitive to acidification, considerable damage has already occurred, or is expected, given estimated 1980 levels of acidic deposition. Emission reduction strategies have been proposed to minimize or reverse this damage (e.g. Young 1988). The regional model is useful in evaluating how much benefit we might expect from implementation of such strategies.

We have examined three emission scenarios which, together with the baseline (1980) scenario presented earlier, can be used to examine the predicted consequences of alternative emissions control policies. Estimated emissions for 1980 are presented in Table 5. The first control scenario ("Canada-only") involves reducing overall emissions in eastern Canada by 42% from 1980 levels, as described in Young (1988). The second ("Canada and United States") allows for a uniform 42% reduction of all United States sources in addition to the Canadian controls. The

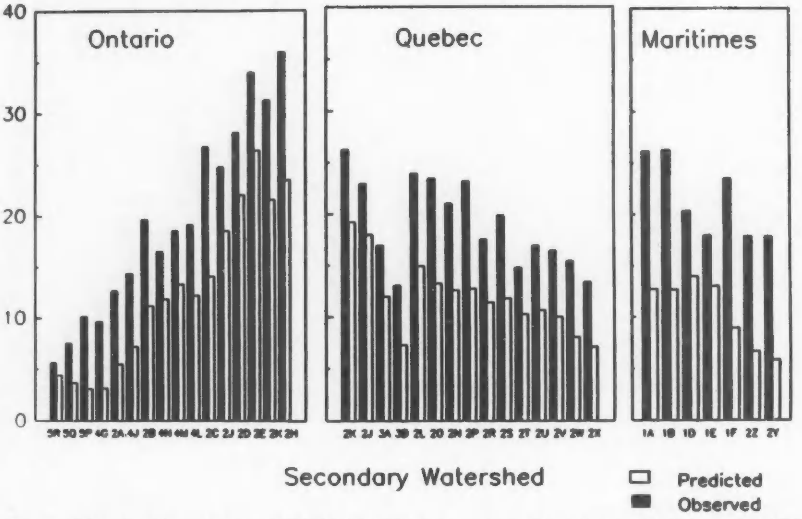

FIG. 4. Estimated (from observed CAPMoN 1980 data) and predicted (interpolated from the AES-LRTAP model of Olson et al. (1983)) 1980 wet sulphate deposition for secondary watersheds throughout eastern Canada.

third represents a 10% increase in emissions from all source regions and is intended to simulate a worst case scenario.

Wet sulphate deposition values predicted for each secondary wateshed, using 1980 emissions data and the transfer matrix, were consistently lower than observed values (Fig. 4). This is to be expected, since the model upon which the transfer matrix is based does not include sulphur derived from nonanthropogenic, or non-North American sources. The difference between predicted and observed values can be considered "non controllable" sulphate deposition. Since the magnitude of this component should not be affected by emission controls, its value can be used directly to correct the predicted sulphate deposition for the other three scenarios. Thus, the deposition values used for each scenario in the regional model were given by the sum of the interpolated value from the transfer matrix output, and the difference between the 1980 observed value and the 1980 predicted value. Generally, greatest reductions (or increases) in deposition are predicted in the southern watersheds in each region, with the greatest absolute changes occurring in Ontario (i.e. 2D, 2E, 2H, 2K; Fig. 5).

There are many facets to the results for the four scenarios. Three aspects are presented here. First, we contrast median alkalinity and pH values by watershed and scenario (Table 6). Second, we show the predicted proportions of lakes with eventual alkalinities <0 $\mu eq \cdot L^{-1}$, and with eventual pH less than 5.0, 5.5, and 6.0 (Table 7). Finally, we present quantile–quantile plots (Fig. 6, 7) which show the shifts in alkalinity and pH distributions, due to different deposition scenarios relative to original conditions. Predictions are viewed on eastern Canadian and regional scales, and for specific secondary watersheds to highlight various aspects of the results.

Comparison of median alkalinity and pH values shows that improvements in regional lake chemistry expected to result from emission controls are typically small relative to the changes that have occurred (Table 6). With no emission controls in place, we predict, for all of eastern Canada, a decrease in median alkalinity from original to eventual state of 21 $\mu eq \cdot L^{-1}$. With the proposed Canada-only controls, the decrease is reduced to 17 $\mu eq \cdot L^{-1}$, a 19% improvement relative to the losses in the absence of such controls. Combined Canada and United States controls reduce the damage to 14 $\mu eq \cdot L^{-1}$, a 33% improvement. A 10% increase in emissions would reduce median alkalinity by 1.0 $\mu eq \cdot L^{-1}$. Median pH shifts are small.

In Ontario, none of the three emission scenarios produces a considerable change in median alkalinity and pH on the provincial scale, because the population of lakes includes many with high alkalinity. In Quebec, the effect of Canada-only controls is somewhat greater than the incremental effect of adding United States controls. In the Maritimes, the two strategies have comparable effects.

In specific secondary watersheds, there are a variety of responses to the two emission control scenarios. For instance, in the Sudbury area of Ontario (2C), the increase in median alkalinity, due to the Canada-only controls, is small (5 $\mu eq \cdot L^{-1}$) relative to the effect of additional United States controls (11 $\mu eq \cdot L^{-1}$). In the Quebec Laurentians (2S), the opposite is true: Canada-only controls produce an increase of 5 $\mu eq \cdot L^{-1}$ whereas the addition of United States controls adds only 2 $\mu eq \cdot L^{-1}$ to the median value. In southwest Newfoundland (2Y), the changes due to controls are smaller, but the pattern is similar to that for 2S. Thus, the relative benefits of Canada-only versus Canada–United States emissions controls vary regionally across eastern Canada. The benefits of regionally uniform emission controls are not evenly distributed.

The examination of median values does not reveal all aspects of the results, especially in Ontario. Several chemical thresholds for damage have been put forward in the literature. We consider four examples here: alkalinity <0 $\mu eq \cdot L^{-1}$, pH less than 5.0, 5.5, or 6.0. Again, the results vary considerably among watersheds (Table 7).

The relative benefits of different emission scenarios depends on the chemical criterion selected to measure the impacts. This is true at secondary watershed and provincial scales for both alkalinity and pH criteria. To illustrate this, consider the change

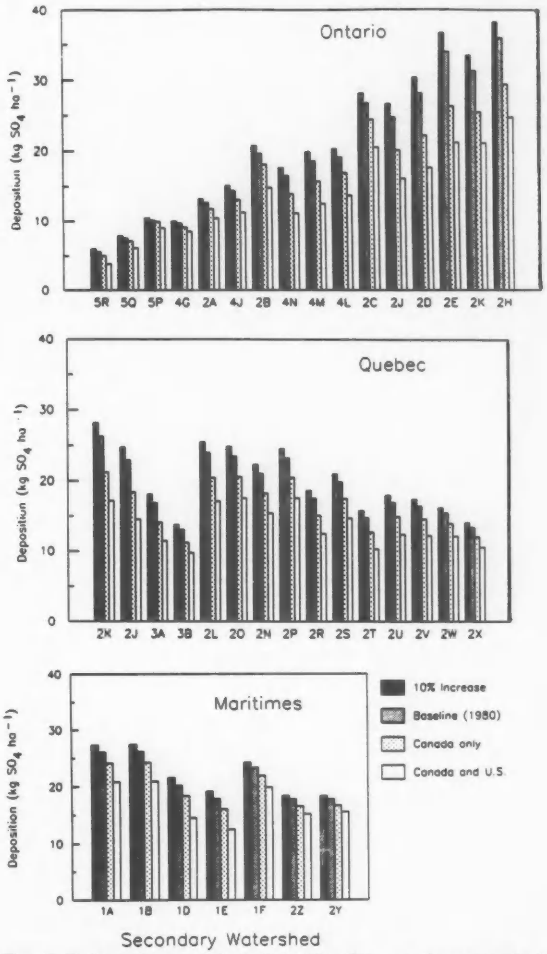

FIG. 5. Estimated wet sulphate deposition for secondary watersheds throughout eastern Canada, for the four emissions scenarios applied to the regional model. See text for further explanations of these scenarios. (A) Ontario; (B) Quebec; (C) Maritimes.

in the proportion of lakes exceeding a particular criterion as Canada-only controls are implemented (compare columns 1 and 2 of Table 7), in contrast to the change seen when United States controls are added (compare columns 2 and 3). In Quebec, Canada-only emission controls are predicted to have a greater effect than the addition of United States controls, when alkalinity <0.0 is the criterion (2.8 versus 1.8%). The opposite is true when pH < 5.0 is the criterion (1.2 versus 1.3%). In watershed 2S, Canada-only controls and additional United States controls have comparable effects when alkalinity <0 is used as the metric (4.0 versus 4.1%), while the additional United States controls have a much greater influence on the proportion of lakes with pH <5.5 (4.1 versus 8.5%).

Selection of these chemical criteria is linked to the perceived requirements of aquatic biota. Lakes with alkalinity less than zero, or pH less than 5.0, generally have greatly impaired biotic communities, and very few valued fish species can persist in such waters (Baker 1984). Kelso et al. (1986), however, have shown in field surveys that biotic diversity of several taxonomic groups is lower in lakes with pH less than 6.0. Eilers et al. (1984) have compiled biotic pH-minima curves, showing a decrease in the proportion of species than can be expected to persist as pH values range from 7.0 down to 4.0, with the most rapid declines being in the range 4.5–6.0. Mills et al. (1987) and Schindler et al. (1985) have described the results of experimental lake acidification, showing how various biota, including fish, disappeared from a lake as the pH was lowered from above 6.5 to 5.0.

These observations suggest that a single threshold value (i.e. critical acid sulphate loading rate) for determining the ecological impact of acidification is inadequate. Rather than cite predicted impacts for a range of loading rates, we must devise ways of combining chemical impact results or develop integrated measures of biological damage.

One such approach to integrated chemical assessment involves the use of quantile–quantile graphs in which quantiles of original and eventual cumulative distributions of pH or alkalinity were plotted against one another. To illustrate the use of such graphs, consider Fig. 6 where the original distribution of pH for eastern Canada is compared with the eventual distribution given 1980 deposition rates. The X and Y axes have the same scale. This was achieved by plotting the quantiles of the original pH distribution against themselves, giving a straight diagonal line (line a in Fig.6A). The X-axis was then relabelled to show a subset of the percentiles (e.g. the 5th percentile lies at about pH 6.1 on the original cumulative distribution). Next, the percentiles of the eventual cumulative distribution were plotted against the corresponding percentiles of the original distribution (line b in Fig.6A). The pH decline for lakes can then be shown by dropping a vertical line from line a to line b. The cumulative percentile point is held constant and the shift in pH noted. Thus, the regional model predicts that the pH of about 4% of the lakes changed from <6.0 to <4.8 and that about 40% changed from <6.5 to <6.3 (lines i and ii in Fig. 6A) between original and eventual conditions. Changes in the cumulative percentage of lakes lying at or below any particular pH can be estimated by drawing a horizontal line from line a to line b (Fig. 6B). Thus, the regional model predicts that the percentage of lakes with pH's <6.5 changed from about 40 to about 55, and those with pH's <6.0 changed from about 3 to about 20 (lines i and ii in fig. 6B) between original and eventual conditions.

The shifts of cumulative distributions of lake pH, between original and eventual conditions, are not simply a movement of the distribution along a pH axis. If that were the case, the quantile–quantile lines would be straight and parallel to line a in Fig. 6. Given that the pH distribution is the result of summing over several variable distributions, representing populations of lakes, which interact in differing ways with the model equations at different levels, portions of the distribution move differing amounts, thereby reshaping the distribution (line b in Fig. 6). We cannot assume that a lake which lay at the 5th or 20th percentile originally will still be there after a deposition scenario is imposed. Individual lakes may move either way along the distribution, depending on how they interact with the site model. The regional model does not allow for the tracking of individual lakes, but is focused on the population of lakes in a region, as represented by distributions of characteristics.

Several scenarios can be compared in single graphs for alkalinity and pH, by plotting quantiles for each scenario against those of the original cumulative distribution. This is illustrated

TABLE 6. Predicted median alkalinity and pH values by scenario: aggregate results for all of eastern Canada; aggregated results for Ontario, Quebec, and the Maritimes; and selected results for individual secondary watersheds.

Watershed/Region	Original	Baseline: 1980 emissions	Canada only: 42% cut	Canada and U.S. 42% cut	Emissions increase by 10%
Median predicted eventual alkalinity ($\mu eq \cdot L^{-1}$)					
Eastern Canada	91	70	74	77	69
Ontario	295	300	299	298	300
Quebec	86	58	64	68	56
Maritimes	75	55	57	59	54
2C (Sudbury)	83	35	40	51	31
2S (Laurentians)	77	47	52	54	44
2Y (Newfoundland)	91	76	78	79	76
Median predicted eventual pH					
Eastern Canada	6.57	6.46	6.48	6.48	6.43
Ontario	7.09	7.09	7.09	7.09	7.09
Quebec	6.54	6.40	6.40	6.43	6.35
Maritimes	6.47	6.33	6.35	6.37	6.33
2C (Sudbury)	6.50	6.13	6.21	6.30	6.12
2S (Laurentians)	6.46	6.27	6.31	6.34	6.24
2Y (Newfoundland)	6.55	6.48	6.49	6.50	6.48

for the whole of eastern Canada in Fig. 7. These graphs show the predicted impact of emission controls and emissions increases, compared with the predicted impact of 1980 deposition levels. Here, the approximate positions of the cumulative percentiles are shown above the straight diagonal line with vertical dashed lines drawn to intersect the scenarios (Fig. 7). The graphs show that more than 70% of lakes are predicted to have lower alkalinities and pH's (Fig. 7A and B). Lakes with original alkalinities above about 175 $\mu eq \cdot L^{-1}$ show increases in the four scenarios relative to original conditions. This phenomenon was discussed earlier. The changes in the distributions for the Canada-only and Canada and United States emission controls, and the 10% emission increase are small compared with the change between original and 1980 conditions. The control strategies produced the greatest recovery in lakes with the lowest original alkalinities and diminishing recovery at higher alkalinities (Fig. 7A). About 10% of lakes show 0.1–0.2 pH unit increases under each of the control strategies (Fig. 7B). The scenario where emissions were increased by 10% results in a small shift to lower pH's. About 10% of the lakes are predicted to have alkalinities <0.0 $\mu eq \cdot L^{-1}$ as a result of acidic deposition, and the percentage is predicted to shift to <5, as a result of emission controls. A majority of lakes, however, show only marginal improvement. About 40% of lakes, which had an original pH of 6.5 or less, are predicted to still have more than 0.1–0.2 pH unit depression after a 42% reduction of emissions in both eastern Canada and the United States.

Discussion

Overall, the results of applying the regional model suggest that substantial impacts have already occurred or are expected to occur, given current (1980) levels of emissions. Throughout sensitive areas of eastern Canada, we estimate (Table 7) that 4.3% of all lakes will become acidic (defined as predicted pH less than 5.0) at 1980 levels of emissions. Although the total number of lakes in sensitive regions of eastern Canada remains a matter of some debate, we believe that 4.3% translates into a minimum of 20 000 lakes. Furthermore, proposed emissions control strategies are only expected to reduce this value to approximately 3.0% (Canada-only controls) or 1.9% (Canada and United States controls), values which still translate into thousands of lakes.

Other estimates of current damage, or expected future changes, for sensitive regions of eastern North America are comparable with ours. Kelso et al. (1986) estimated that there are currently over 14 000 acidic lakes in eastern Canada (pH less than 4.7). Schindler et al. (1989) used a model very similar to ours to show that median alkalinities for lakes in the northeastern United States are 22–55 $\mu eq \cdot L^{-1}$ lower than estimated original values. For the United States upper midwest, Schnoor et al. (1986) estimated that up to 30% of the lakes in the region would be acidified (alkalinity less than 0), by deposition rates comparable with those experienced in the Adirondacks.

While the impacts predicted by this model may seem extreme, there are a number of reasons for believing the estimates are in fact conservative. Our empirical pH–alkalinity curve tends to overestimate pH at low alkalinity (Marmorek et al. 1990). As noted earlier, we have adopted conservative assumptions in judging the values of b in the $F_w - [C_B]_o$ relationship and $[SO_4]_0$. Furthermore, we assume no erosion of a catchment's acid neutralization capacity over time (declining F_w), thereby ignoring the possibility of increased acidification due to a "delayed response" (Cosby et al. 1985). Finally, we assume that the acidification process is completely reversible, such that recovery will occur in direct relation to reductions in acidic sulphate deposition.

On the other hand, there are three possible reasons why the estimates might be excessive. First, there are processes not included in the model that will tend to reduce rates of acidifi-

TABLE 7. Proportion of lakes with predicted eventual alkalinity <0., or pH <5.0, 5.5, or 6.0, for selected regions, under four alternative acidic sulphate emissions scenarios.

Watershed/Region criterion	Baseline: 1980 emissions	Canada only: 42% cutback	Canada and U.S.: 42% cutback	Emissions increased by 10%
Eastern Canada				
Alk < 0.	0.073	0.054	0.037	0.083
pH < 5.0	0.043	0.030	0.019	0.051
pH < 5.5	0.093	0.073	0.050	0.104
pH < 6.0	0.197	0.169	0.143	0.213
Ontario				
Alk < 0.	0.075	0.058	0.039	0.082
pH < 5.0	0.064	0.046	0.030	0.071
pH < 5.5	0.082	0.065	0.046	0.089
pH < 6.0	0.115	0.097	0.076	0.122
Quebec				
Alk < 0.	0.072	0.044	0.026	0.089
pH < 5.0	0.037	0.025	0.012	0.047
pH < 5.5	0.103	0.070	0.039	0.120
pH < 6.0	0.256	0.209	0.169	0.280
Maritimes				
Alk < 0.	0.072	0.062	0.046	0.077
pH < 5.0	0.036	0.027	0.018	0.043
pH < 5.5	0.090	0.081	0.064	0.097
pH < 6.0	0.188	0.172	0.156	0.201
2C				
Alk < 0.	0.279	0.246	0.185	0.298
pH < 5.0	0.239	0.205	0.160	0.260
pH < 5.5	0.304	0.271	0.207	0.322
pH < 6.0	0.427	0.386	0.314	0.451
2S				
Alk < 0.	0.233	0.193	0.152	0.241
pH < 5.0	0.189	0.148	0.063	0.199
pH < 5.5	0.253	0.223	0.186	0.277
pH < 6.0	0.407	0.382	0.345	0.424
2Y				
Alk < 0.	0.069	0.062	0.051	0.073
pH < 5.0	0.040	0.032	0.026	0.045
pH < 5.5	0.082	0.076	0.068	0.087
pH < 6.0	0.173	0.167	0.156	0.183

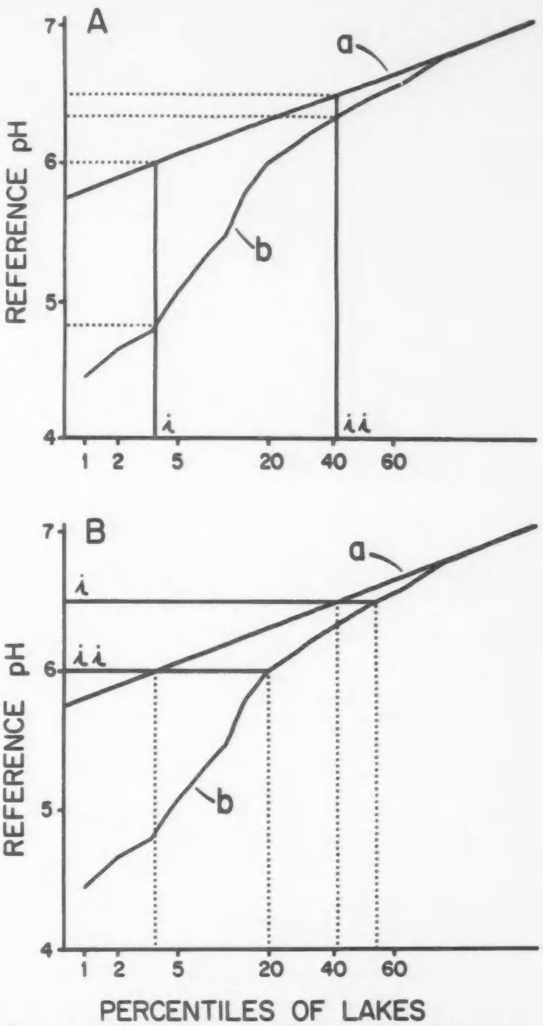

FIG. 6. Quantile–quantile graphs of the cumulative distributions of original and eventual (given 1980 deposition rates) pH. (A) Examples i and ii show the change in threshold pH's for given percentiles of lakes. (B) Examples i and ii show the change in percentiles for given threshold pH's. Lines *a* and *b* are the graphs of original versus original and original versus eventual conditions for the cumulative distributions of lake pH. The X axis is relabelled to show selected percentiles rather than pH.

cation. Most notably, mineral adsorption of sulphate within the lake's catchment has been shown to reduce the flux of acidity to surface waters (Johnson and Cole 1977; Singh et al. 1980). The sulphate adsorption capacity of soils in glaciated regions (including Canada) is thought to be relatively low, however (Rochelle and Church 1987). As well, this process will only delay the acidifiction of surface waters, not prevent it. Once the sulphate levels in soil solutions approach equilibrium with sulphate deposition, "breakthrough" occurs and surface water [SO_4] increases concurrently with declines in alkalinity (Johnson and Reuss 1984).

Second, in many lakes in eastern Canada, organic acidity contributes significantly to the alkalinity deficit. By ignoring organic anions in our model, we overestimate the original alkalinity of these lakes and, thus, provide a misleading impression of how "pristine" conditions were historically. Organic and mineral acidity are additive, however (Gorham et al. 1986; Brakke et al. 1987), so that even naturally acidic lakes will experience declines in alkalinity with increasing acidic deposition. Thus, our predicted changes in alkalinity, (but not pH) will not be affected by ignoring organic anions. In addition, other studies have not found any association between organic anions and lake alkalinity, on a regional basis (Jeffries et al. 1986; LaZerte and Dillon 1984). In the upper midwestern region of the United States (an area receiving sufficiently low levels of acidic sulphate deposition to be considered a reference region), the Eastern Lake Survey found that of 324 lakes with DOC >6 $mg \cdot L^{-1}$, only six had alkalinities less than zero. These considerations suggest that the exclusion of organic anions from our model is not a major source of errors in our predictions of damage.

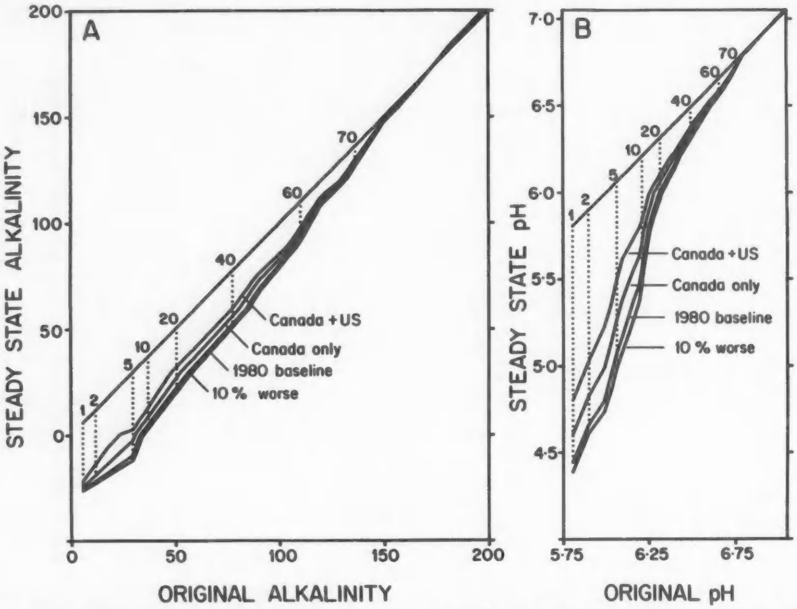

FIG. 7. Quantile–quantile graphs of alkalinity (A) and pH (B) for all lakes in eastern Canada. The cumulative distributions of original conditions and eventual conditions for the four scenarios (1980 baseline, Canada-only, Canada and United States, 10% increase) are plotted by percentile against the distribution of original conditions. The numbers above the straight diagonal are the cumulative percentiles; dashed lines are dropped vertically from these percentiles to intersect the scenario lines.

Third, there is accumulating evidence from paleolimnological studies (Davis et al. 1985), regional surveys (Jeffries et al. 1986), intensive monitoring (Dillon et al. 1987), laboratory studies (Almer et al. 1978), and experimental manipulations of lake or precipitation chemistry (Schindler 1980; Yan and Dillon 1984; Wright 1987), that lake acidification may be associated with increased transparency and/or a loss of DOC from surface waters (this evidence was reviewed by Marmorek et al. (1988)). This change is thought to be most likely due to complexation of organic ligands by aluminum (e.g. Driscoll et al. 1986). A portion of sulphate deposition may, therefore, be consumed in increasing aluminum and removing DOC, rather than reducing alkalinity.

The model described in this and the companion paper represents an approach that is unique, at least in North America. Other regional modelling efforts in North America are either not designed tc examine the consequences of alternative control strategies (e.g. Schindler et al. 1989; Rogalla et al. 1986; Schnoor et al. 1986) or do not predict the consequences of control measures, in terms of ecological damage (e.g. Shaw 1986; Young and Shaw 1986). In contrast, the RAINS model (Alcamo et al. 1987) is designed to serve a similar purpose for Europe. In a subsequent paper, we will present the results of using this model to estimate biological damage due to acidification (C. K. Minns, unpubl. data).

The results presented here suggest that existing control proposals are both inadequate and regionally uneven. The proposed strategies are highly simplistic, especially in that they do not allow for regional variations in the degree of control imposed. Model predictions imply that reductions of 42% in acidic sulphate emissions are likely unnecessary in some regions, but are inadequate in others. Methodologies exist for determining more optimal control strategies given certain constraints and objectives, which would concentrate control efforts in areas where they are needed most (e.g. Shaw 1986; Young and Shaw 1986). These methods should be explored using models that include ecological damage indicators and then interpreted in the context of other (social, political, economic) considerations. Preliminary exploration of scenarios which limit deposition above a critical threshold in each subregion (Minns and Kelso 1986), indicate that this strategy is far more cost effective (at least when measured in terms of the number of lakes restored to pH >5.0 per ton of sulphur removed from emissions).

Finally, it would be misleading to convey, albeit unintentionally, the impression that the damage estimates presented in this paper can be tabled with a specified degree of confidence. The model includes a number of key assumptions, some of which are impossible to verify with existing data. The representativeness of the regionalization database cannot be demonstrated, even though there are no compelling reasons to expect major biases that would give rise to overestimates of impacts (except for Nova Scotia, where we have made a conservative correction).

Ideally, it would be preferable to have a verified model to use as the basis for determining both impacts and optimal control strategies. Given the urgency of the acid rain problem (at least as perceived by some parties), however, postponing decisions until such models are available is not an option. In fact, postponement is itself implicitly a decision. Verifying model predictions will require long term monitoring data collected over a period of several decades, by which time further damage is likely to have occurred.

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Many scientists contributed to the development of the model described in the paper. Their names are listed in an Appendix to the companion manuscript. D. W. Schindler and three anonymous reviewers provide numerous useful comments on an earlier draft. Audrey Chui assisted with the preparation of the figures. J. E. Moore assisted with the quantile–quantile analysis. The work was funded in part by contracts from the Department of Fisheries and Oceans Canada, Environment Canada, and the Federal Government Unsolicited Proposal Fund to ESSA Ltd.

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Spatial and Temporal Distribution of Sub-Ice Macrofauna in the Barrow Strait Area, Northwest Territories

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The distribution of sub-ice macrofauna was investigated in the Barrow Strait area near Resolute, N.W.T. from April–June, 1985, 1986, and 1987, and in January 1986. Invertebrates were sampled using remotely deployed net and video camera systems. Ten species of amphipods and two species of mysids were found, but over 90% of the biomass was made up of only four species of amphipods: *Weyprechtia pinguis*, *Onisimus litoralis*, *Gammarus setosus*, and *Onisimus* spp. juveniles. Species composition varied annually, with *W. pinguis* dominating in spring 1985, *O. litoralis* in 1986, and *G. setosus* in 1987. There were also areal differences in species composition over distances of 50–200 km. Underlying water depth was the major environmental correlate of both total biomass and species composition; total biomass decreased with increasing underlying water depth, being near zero over >100 m depth. We hypothesize that spring sub-ice distribution is a reflection of summertime benthic distribution. Total biomass decreased with increasing snow depth early in the spring, probably because the attenuation of incident light by snow reduces the concentration of sub-ice algae. Total biomass was lower within 1 km of the ice edge than in areas further from the ice edge.

La répartition de la macrofaune vivant sous la glace a fait l'objet d'une étude dans la région du détroit de Barrow, près de Resolute, T.N.-O., entre avril et juin 1985, 1986 et 1987, ainsi qu'en janvier 1986. Les invertébrés ont été échantillonnés à l'aide d'un filet déployé à distance et d'un système de caméra vidéo. Dix espèces d'amphipodes et deux espèces de mysides ont été recensées, mais plus de 90 % de la biomasse étaient constitués de seulement quatre espèces d'amphipodes : *Weyprechtia pinguis*, *Onisimus litoralis*, *Gammarus setosus* et *onisimus* spp. juvéniles. La composition des espèces variait d'une année à l'autre, *W. pinguis* dominant au printemps 1985, *O. litoralis* en 1986 et *G. setosus* en 1987. On a également relevé des différences géographiques dans la composition des espèces sur des distances de 50 à 200 km. La profondeur de l'eau sous-jacente était le principal corrélat environnemental tant de la biomasse totale que de la composition des espèces; la biomasse totale diminuait de façon inversement proportionnelle à la profondeur de l'eau sous-jacente et se situait à près de zéro à plus de 100 m de profondeur. Les auteurs ont fait l'hypothèse que la répartition printanière sous la glace reflète la répartition benthique estivale. La biomasse totale diminuait de façon inversement proportionnelle à la profondeur de la neige au début du printemps, probablement parce que l'atténuation de la lumière incidente par la neige réduit la concentration des algues sous la glace. La biomasse totale était moins abondante à moins de 1 km de la bordure de glace que dans les zones plus éloignées de la bordure.

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The soft undersurface of spring sea ice forms a temporary habitat for a large and diverse community of organisms that are benthic or pelagic at other times of the year. An algal layer, composed principally of diatoms (Dunbar and Acreman 1980; Hsiao 1980), is linked trophically to a community of invertebrates whose macrofaunal component is composed mainly of gammarid amphipods and mysids (Bradstreet and Cross 1982; Grainger et al. 1985). This sub-ice macrofauna is in turn utilized by seabirds (Bradstreet 1980), ringed seals (*Phoca hispida*) (Bradstreet and Cross 1982), Arctic cod (*Boreogadus saida*) (Craig et al. 1982; Lowry and Frost 1981), and anadromous Arctic char (*Salvelinus alpinus*) (Grainger 1953; Moore and Moore 1974).

There is evidence that the sub-ice macrofauna may be particularly vulnerable to disturbance by industrial development in the north (Cross and Martin 1983), but not enough is known about their distribution to be able to predict the ecological consequences of anthropogenic impacts. Here we present findings from 3 yr of study on the effects of environmental factors on species composition and biomass distribution of the sub-ice macrofauna. Annual, seasonal, and shorter-term changes and their relationships to environmental change are also described.

Materials and Methods

Site Description

Fieldwork was performed near Resolute, N.W.T. (74°42′N, 94°50′W, Fig. 1) on Barrow Strait from March to July, 1985 to 1987, and in January 1986, entirely on first-year sea ice.

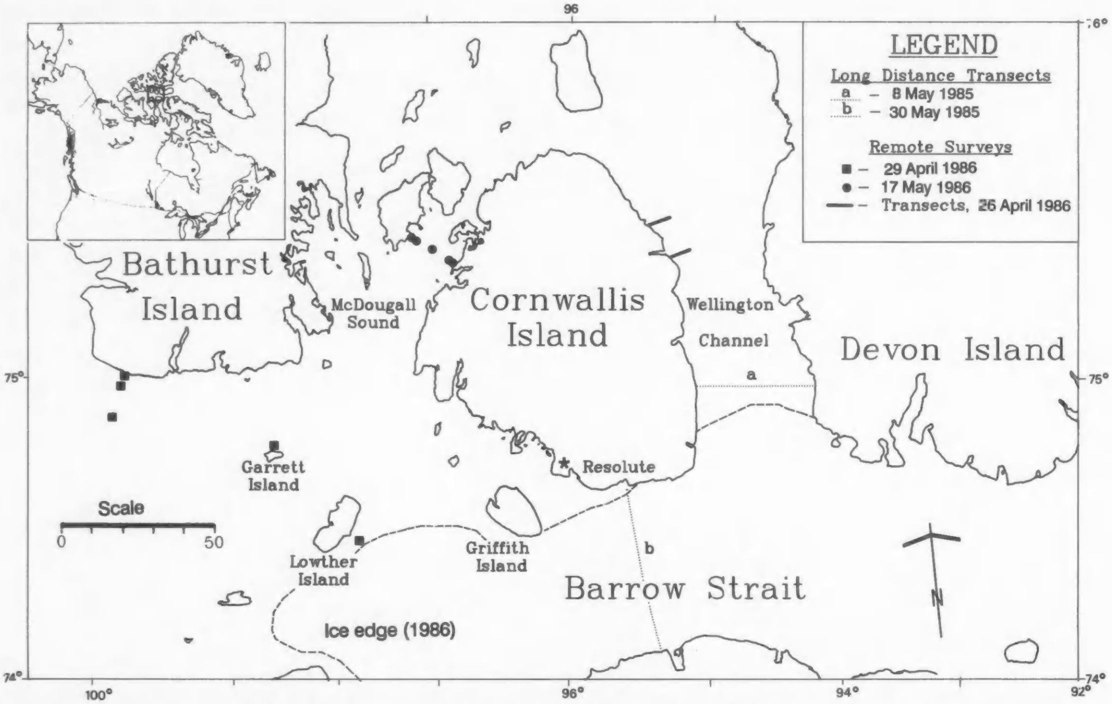

FIG. 1. Location of study area, long distance transects sampled in 1985 and stations sampled in 1986 remote surveys. The entire sea was covered by shore-fast ice in 1985; in 1986 the ice-edge was as indicated, with the SE portion of Barrow Strait covered by broken first-year ice.

Barrow Strait is covered by landfast first-year ice from freeze-up in October until breakup in late July. Multi-year ice occurs only in small, isolated patches. In some years, as in 1986, the Lancaster Sound shorelead (an extension of the North Water polynya) extends as far west as Griffiths Island, within 10 km of Resolute (Smith and Rigby 1981). Maximum ice thickness in early May ranges from 1.7 to 2.4 m. The ice varies in roughness; typically, pans of smooth ice ranging in size from a few hectares to many square kilometres are surrounded by pressure ridges and areas of rough, jumbled ice. Smooth ice predominates and in some years, rough ice may be present only in nearshore areas. Snow cover is wind-packed and drifted, ranging from 0 to 50 cm in depth. Growth of the sub-ice algae begins in mid-February with the end of the polar night. Maximum ice algal biomass is reached in early June, after which the algal layer begins to slough off (H. E. Welch, unpubl. data).

Field Methods

Invertebrates were sampled with a sweep net (mesh size 500 μm) and observed with a video camera system. Divers observed that the area sampled by either device was not disturbed by the drilling of the sampling hole. The sweep net (Fig. 2) was deployed through a 25-cm diameter hole and sampled a doughnut-shaped area, scraping invertebrates off the undersurface of the ice. An identical area (5.9 m^2) was swept by the net for each sample, and we assumed that catch was proportional to density.

The video camera system (Fig. 3), consisting of an Osprey OE 1321 camera, control and pan-tilt units, and a Panasonic recorder and video monitor, was deployed through a 46-cm diameter hole. Divers observed that the camera itself caused no apparent disturbance except for a small release of bubbles when first deployed; the affected area was not used in amphipod density estimates. Distance between the camera and the sub-ice surface was adjusted to 27 cm (±5% as measured by divers). The arm was rotated slowly, stopping briefly at 20 equally spaced intervals along the circumference traversed by the camera. One video "sample" consisted of 20 video images, all subtending areas of equal size. This area was calculated by measuring a sub-ice target of known size.

Five types of surveys were carried out (Table 1, Figs. 1 and 4) over the years 1985–87. Baseline survey data came from the Resolute area surveys, whose numbers and transect locations varied between years according to ice conditions. Sampling stations were located at predefined distances along each transect, and the drillsite at each station was randomly located. The general applicability of the Resolute area surveys was determined by comparison with data collected during the remote surveys. Small scale and short-term variation surveys were designed to assess spatial and temporal heterogeneity. Multiple sweep net samples were taken from a 100 × 100 m area during small scale surveys, while a short-term variation survey consisted of repeated sampling over a full tidal cycle at one station with the camera system. Video camera surveys were designed to calibrate the sweep net. Sweep net samples were taken from the same hole immediately after camera sampling.

At each sampling site, snow depth (±1 cm) was measured at one pace intervals around the circle overlying the sweep net or camera path, and ice thickness (±1 cm) measured in the

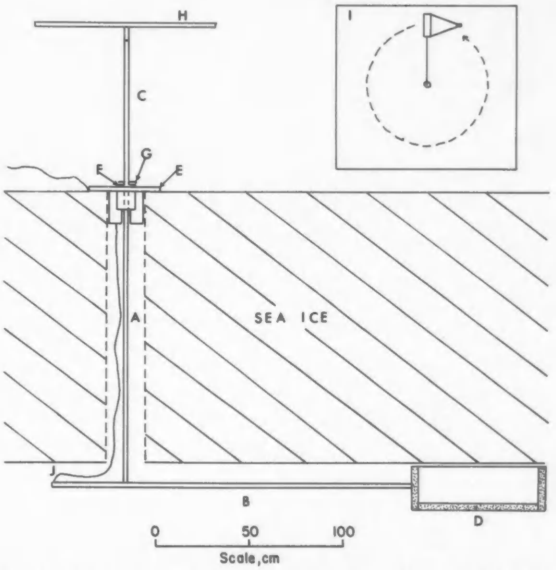

FIG. 2. The sweep net is pushed through the sampling hole (A) with the horizontal arm (B) extended to a position parallel to that of the vertical arm (C). Once the horizontal arm is through ice, floatation on the net frame (D) causes it to float up against the sub-ice surface. The base (E) and insert (F) are placed over the vertical arm and set into the sampling hole, and a pin (G) placed through a hole in the vertical shaft prevents it from falling through the sampling hole. The T-handle (H) is placed over the vertical shaft, and the net is rotated one complete circle around the sampling hole ((I) — looking up at the sub-ice surface). The net is retrieved by removing the T-handle, base and insert, pushing down on the vertical arm while pulling up on the retrieval rope (J) until the horizontal arm is parallel to the vertical arm, then pulling it out of the hole.

sampling hole. Water depth (± 1 m) was measured by sounding line or echo sounder, and distance from shore was monitored with the snowmobile odometer.

Laboratory Methods

Sweep net samples were returned from the field packed in slush to prevent predation and preserved in 5% freshwater formaldehyde solution within 8 h of capture. Samples were sorted to species and cohort, except for *Onisimus* spp. and *Parathemisto* spp. juveniles which were sorted to genus. *Gammarus setosus* for which cohorts were not identifiable, was sorted into arbitrarily chosen size classes.

Species biomass was estimated using dry weight–length relationships (Table 2). Mean weights for species-cohorts were calculated for the Resolute area survey samples only. Biomass was estimated for samples from other survey types using the mean weights for each species-cohort from the Resolute area survey closest in time. From each survey, a subsample of each species-cohort was chosen randomly, the number of animals from each sample proportional to its contribution to the total. The total number of each species-cohort measured from each survey was 10–20 for smaller amphipods such as *Weyprechtia pinguis* juveniles and 30–40 for larger amphipods such as *Onisimus litoralis*. All individuals of rare species were measured. Species biomass in a sample was estimated by multiplying the number of a particular species-cohort in the sample by its mean weight. Cohorts were then summed for each species.

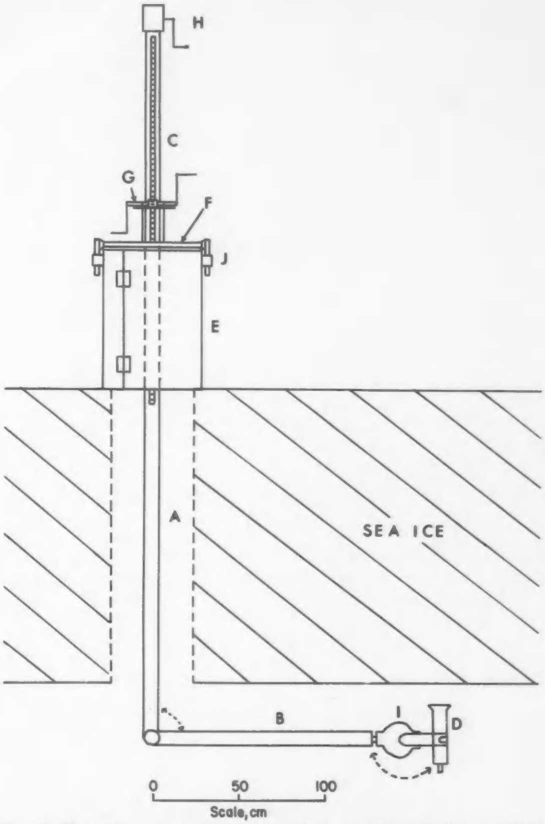

FIG. 3. The video camera system was deployed through the sampling hole (A) with the horizontal arm (B) folded against the vertical arm (C) and the camera (D) pointing parallel to the horizontal arm. The cylindrical base (E), constructed from a 205-L drum split lengthwise and hinged together, was then placed into position beneath the tripod (F). The vertical shaft was lowered into the hole using the crank and toothed rod mechanism (G) until the camera was clear of the bottom of the sampling hole. The horizontal arm was then lowered into the 90° position (as shown) using the crank and chain drive mechanism (H). The camera was oriented using the pan-tilt (I) so that it pointed straight up at the ice (as shown), and the vertical arm was raised until the camera was the required distance from the ice. Finally, the system was levelled by placing a bubble level on the tripod and adjusting the clamps (J).

It was not possible to identify animals in video images, so only total numbers per image were counted. The four images closest to the point where the camera was initially deployed were not used because of possible disturbance effects. Each image covered 0.2 m^2 and 16 images were counted for every station, for a total coverage of 3.2 m^2.

Statistical Methods

Taylor's power regressions (Downing 1979; Green 1979) showed that macrofaunal distribution was aggregated; therefore all species abundance data were log-transformed. The relationship between biomass and the environmental variables meas-

TABLE 1. Sub-ice amphipod surveys, 1985–87.

Survey type	Date	Sampler	No. of samples
Resolute area surveys	9–17 May 1985	Sweep net[a]	58
	4–13 June 1985		50
	13–17 January 1986		13
	19–24 April 1986		50
	10–16 May 1986		67
	31 May–4 June 1986		67
	21–26 June 1986		65
	29 April–6 May 1987		47
Remote surveys	26 April 1986	Sweep net	14
	29 April 1986		18
	17 May 1986		15
Small scale surveys	9 May 1986	Sweep net	16
	29 May 1986		20
Video camera surveys	1–8 May 1986	Video camera and sweep net	13
	20–27 May 1986		17
	11–16 May 1986		14
Short-term variation experiments	9 June 1986	Video camera	4
	14 June 1986		4

[a] Two versions of the sweep net were used, one up to and including January 1986, the other in spring 1986 and 1987. Only the later version was calibrated.

TABLE 2. Dry weight–length relationships. Equations are of the form: Ln [dry weight (mg)] = a[Ln(head length (mm))] + b.

Species	N	r^2	a	b	Source
Onisimus litoralis[a]	50	0.93	3.410	2.617	This study
Weyprechtia pinguis	85	0.98	3.397	0.394	This study
Gammarus setosus	52	0.99	3.515	0.809	This study
Apherusa glacialis	40	0.72	3.292	1.252	This study
Ischyrocerus anguipes	30	0.87	3.636	0.565	This study
Gammarus wilkitzkii	16	0.96	3.419	0.845	This study
Gammaracanthus loricatus	9	0.95	2.586	0.167	This study
Parathemisto spp. juveniles[b]	150	0.98	2.793	5.348	Percy and Fife 1983
Mysis oculata[b,c]	?	0.94	2.35	0.011	Bradstreet 1980

[a] Also used for *Onisimus glacialis*, *Onisimus nanseni*, and *Onisimus* spp. juveniles.

[b] Equation of the form: Log10[dry weight (mg)] = a[Log10(total length (mm))] + b.

[c] Also used for *Mysis polaris* and *Mysis litoralis*.

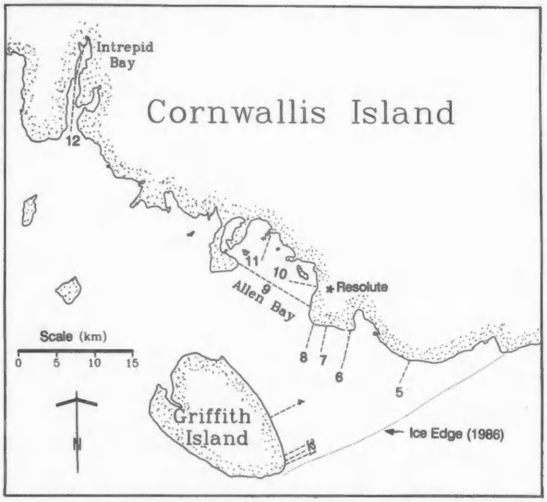

FIG. 4. Locations of transects sampled was in Resolute area survey's. Transect 7 was sampled in January 1986; the rest were sampled in spring. 1–3 = 1986; 4, 5, 6, 8 = 1985–87; 9 = 1986–87; 10 = 1987; 11 = 1985–86; 12 = 1985.

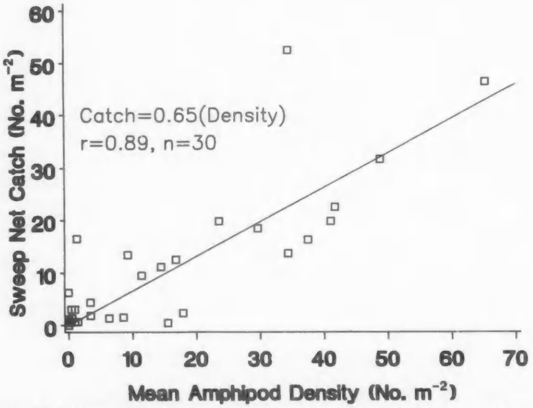

FIG. 5. Relationship between sweep net catch and sub-ice amphipod density as determined with the video camera system.

ured was evaluated from scatterplots of log-transformed total biomass and specific variables and with multi-linear regression (SAS Institute 1982). Sampling sites were coded as dummy variables to see if spatial differences in biomass not accounted for by the environmental variables were explained by location. The best regression model was chosen as that equation which: (i) maximized r^2, and (ii) exhibited partial probabilities p>0.05.

Individual species abundances were assumed to respond to underlying environmental gradients in a nonlinear fashion (Gauch 1982; Green 1979). Reciprocal averaging (RA) (Hill 1973), an ordination technique closely related to principal components analysis, was used to determine which environmental factors were related to species distribution. RA produces simultaneous ordinations of species and samples, and has been found to be the most successful of the metric ordination methods in retrieving at least the rank order of sites on environmental gradients in real and simulated ecological data (Fasham 1977; Hill 1973; Kenkel and Orloci 1986).

Ordinations were preformed on the log-transformed species biomass data from the Resolute area surveys and remote surveys using the ORDIFLEX computer package (Gauch 1977). Species occurring in less than 10% of the samples were deleted from the analyses. RA is sensitive to outliers, which may dominate the first few axes, obscuring real trends in the data (Kenkel and Orloci 1986). Therefore, species having distributions obviously disjunct from the others after an initial ordination were deleted. Scatterplots of the RA axis scores against environmental variables were examined visually, and relationships were considered indicative of an environmental gradient controlling species distribution, to be analyzed further by direct graphical methods.

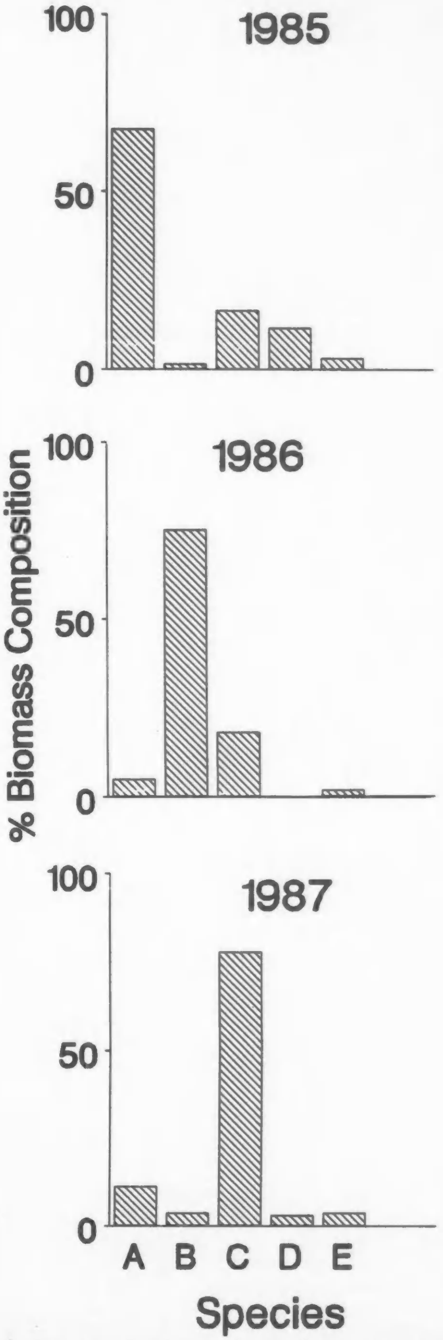

FIG. 6. Sub-ice amphipod species composition in the Resolute area as determined from all Resolute area surveys, spring 1985–87. Species A = *Weyprechtia pinguis*, B = *Onisimus litoralis*, C = *Gammarus setosus*, D = *Onisimus* spp. juveniles, E = Others, including *Gammarus wilkitzkii*, *Ischyrocerus anguipes*, *Apherusa glacialis*, *Parathemisto* spp. juveniles, *Onisimus glacialis* and *Onisimus nansenі*.

TABLE 3. Changes in mean species biomass of sub-ice amphipods between spring 1986 and 1987.

	Mean biomass ($mg \cdot m^{-2}$)	
Species	10–16 June 1986	29 April–6 May 1987
Onisimus litoralis	17.7	0.7[a]
Onisimus glacialis	0.4	0.1[a]
Onisimus nanseni	0.0	0.1
Onisimus spp. juveniles	0.0	0.8[a]
Weyprechtia pinguis	1.8	2.7
Gammarus setosus	1.5	4.2
Gammarus wilkitzkii	0.1	0.1
Apherusa glacialis	0.5	0.6
Ischyrocerus anguipes	0.1	0.2
Parathemisto spp. juveniles	0.0	0.0
Gammaracanthus loricatus	0.0	0.1

[a]Difference significant at $p<0.01$ level.

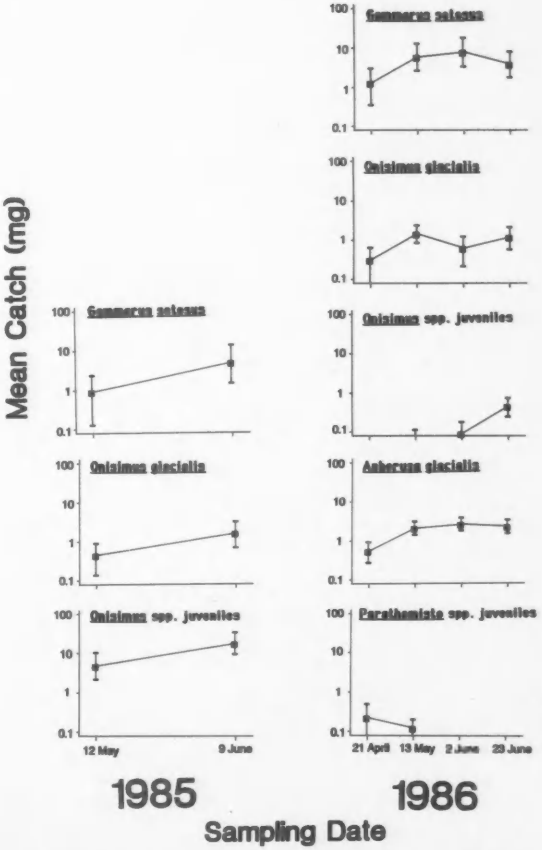

FIG. 7. Change in species biomass over the 1985 and 1986 spring seasons as determined from all Resolute area surveys. Only species that showed significant variations over time are shown.

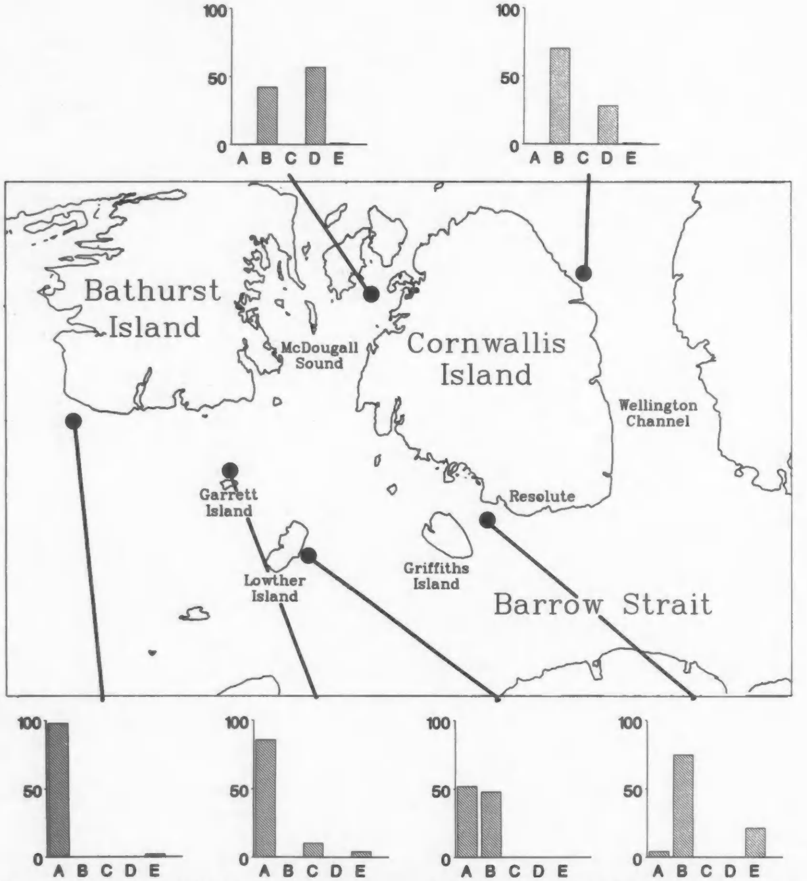

FIG. 8. Species composition of sub-ice amphipods outside the Resolute area as determined from remote surveys, spring 1986. Species A = *Weyprechtia pinguis*, B = *Onisimus litoralis*, C = *Apherusa glacialis*, D = *Mysis* spp., E = others.

Results

Sweep Net Calibration

In spring 1986, video camera stations (Table 1, Fig. 4) were immediately resampled with the sweep net. Regression of sweep net catch against camera counts (Fig. 5) showed that the net efficiency was 65% for densities less than 70 animals·m^{-2} exclusive of juveniles. Juveniles were not included as they were too small to be effectively counted with the camera. At macrofaunal densities greater than 70 animals·m^{-2}, the relationship between total mean density and sweep net catch became nonlinear. The intercept was not significantly different from 0 ($p<0.05$) and regression through the origin (Steele and Torrie 1980) was significant ($p<0.01$) at densities less than 70 animals·m^{-2}. This factor was used to convert the 1986 to 1987 sweep net catches into real density values. The application of this factor probably underestimated true density at sites with densities >70 animals·m^{-2}; however, such sites comprised less than 5% of the total sampled.

Species Composition

The sub-ice macrofauna was composed almost entirely of amphipods in all 3 yr of sampling (Fig. 6). A different species dominated in each year, but the same three species accounted for most of the biomass in all years. Over two-thirds of the biomass was made up of *Weyprechtia pinguis* in spring 1985, with *Gammarus setosus* and *Onisimus* spp. juveniles making up nearly all the remainder. In January 1986, *Onisimus litoralis* was virtually the only amphipod present under the ice, and it dominated the fauna in spring 1986. *Weyprechtia pinguis* was less important, and *Onisimus* spp. juveniles were extremely rare. *Onisimus litoralis, G. setosus*, and *W. pinguis* together comprised over 98% of the sub-ice biomass. In spring 1987, *G. setosus* dominated the community, making up 78% of the total biomass, with *W. pinguis*, *O. litoralis*, and *Onisimus* spp. juveniles comprising most of the remainder.

Annual changes in individual species' biomass could only be calculated between spring 1986 and spring 1987 (Table 3), since the sweep net used in 1985 was slightly different from that used in subsequent years. The abundances of *Onisimus litoralis* and *Onisimus glacialis* decreased greatly from 1986 to 1987, while that of *Onisimus* spp. juveniles increased.

Three species in 1985 and five in 1986 showed significant changes in abundance during the spring season (ANOVA's $p>0.05$) (Fig. 7). In 1985, the abundances of *Onisimus gla-*

TABLE 4. Stepwise multiple regression models relating Ln (total sub-ice amphipod biomass) to environmental and locational variables for all Resolute area surveys. * = coefficient significant at $p<0.05$ level; ** = coefficient significant at $p<0.01$ level; ± = correlation is positive or negative; NS = coefficient not significant ($p>0.05$); O = location not sampled.

	1985		1986					1987
Independent variable	9–17 May	4–13 June	13–17 January	19–24 April	10–16 May	31 May–4 June	21–26 June	29 April –6 May
Water depth	−**	−**	−*	−**	−**	−**	−**	−**
Distance from shore	NS	NS	NS	NS	NS	NS	NS	NS
Snow depth	−*	NS	NS	−**	NS	NS	+**	−**
Ice thickness	NS	+*	NS	−*	NS	NS	NS	NS
12^a	−*	O	O	O	O	O	O	O
11^a	NS	−**	O	NS	−*	NS	+**	−**
8^a	NS	NS	O	−**	NS	NS	NS	NS
1^a	O	O	O	O	−*	−**	NS	NS
2^a	O	O	O	NS	NS	NS	NS	O
3^a	O	O	O	NS	NS	NS	+**	O
4^a	+*	NS	O	O	NS	NS	NS	+*
5^a	NS	NS	O	NS	NS	NS	NS	NS
6^a	NS	NS	O	NS	NS	NS	NS	NS
Wellington channel^b	NS	O	O	O	O	O	OS	O
Barrow strait^b	O	NS	O	O	O	O	O	O
n	58	50	13	50	67	67	65	47
r^2	0.49**	0.73**	0.41*	0.59**	0.50**	0.52**	0.35**	0.66**

[a] Transect location, see Fig. 4.

[b] Long distance transect location, see Fig. 1.

cialis, Onisimus spp. juveniles and *Gammarus setosus* increased from early May to early June. Similarly the abundances of *O. glacialis, Onisimus* spp. juveniles, *G. setosus* and *Apherusa glacialis* generally increased over the course of the spring in 1986. The abundance of *Parathemisto* spp. juveniles decreased from early to late spring in 1986.

In 1986, we found large scale geographical differences in species composition (Fig. 8). Wellington Channel and McDougall Sound had sub-ice communities composed almost entirely of *Mysis* spp. (a mixture of *Mysis oculata* and *Mysis litoralis*), which were very rare in the Resolute area, and *Onisimus litoralis*. There was an east–west trend in species composition, grading from 98% *Weyprechtia pinguis* at western Bathurst Island to approximately equal proportions of *W. pinguis* and *Onisimus litoralis* at Lowther shoal and finally to 75% *O. litoralis* near Resolute (Fig. 8).

Biomass Distribution

Stepwise multiple regressions relating log-total amphipod biomass to environmental and locational variables (Table 4) were significant at the $p<0.05$ level, and regression accounted for 35–73% of the total variance. Underlying water depth was always the most important variable explaining biomass distribution, generally accounting for over half the total variance. Biomass always decreased with increasing underlying water depth. Locational variables were significant in most regressions, but did not reveal any consistent pattern of spatial differences in biomass.

In 1985, snow depth was negatively correlated with total amphipod biomass in early May but not in early June. Ice thickness was positively correlated in June. In January of 1986, water depth alone affected the distribution of sub-ice biomass (no snow was present on the ice at this time). During the spring season, snow depth and ice thickness were negatively correlated with biomass in the first survey in April, but not at any other time. In fact, by mid-June, snow depth had a positive correlation with biomass. The regression for spring 1987 was similar to that for early spring in the two previous years, with snow depth being negatively correlated with amphipod biomass.

Small scale variance surveys also showed that snow depth had a significant effect on biomass distribution, independent of other variables (Fig. 9). Snow depth had a strong negative correlation with amphipod biomass on May 9, 1986, but by May 29, snow depth was positively correlated with biomass (Fig. 4).

Griffith Island stations in the 1986 Resolute area surveys were analyzed as a separate group to determine if the proximity of the ice-edge had any effect on total biomass distribution. Since the slopes of the water depth versus total biomass relationships were the same over the last three survey dates (ANCOVA, $p>0.05$), the data from these surveys were combined to test for ice-edge effects. The data were classified into three groups by distance from the ice-edge: <1 km, 1–2 km, and 10 km. Proximity to the ice-edge has a significant effect on mean total biomass levels (ANCOVA, $p<0.01$). Biomass was lower within 1 km of the ice-edge than in areas farther from the ice-edge (Fig. 10).

Biomass levels in 1985 were not comparable with those of 1986 and 1987 since the sweep net used in 1985 was different from that used in the subsequent 2 yr. Biomass changes between spring 1986 and 1987 in the Resolute area were assessed using ANCOVA with underlying water depth as a covariate. Total amphipod biomass was significantly lower ($p<0.01$) in spring 1987 than in spring 1986 at about the same time (Fig. 11).

Seasonal changes in biomass distribution in the Resolute area were investigated using ANCOVA with underlying water depth as a covariate. In spring 1985, sub-ice biomass was significantly higher in June than in May ($p<0.05$). Mean biomass levels did not change significantly over the first three surveys

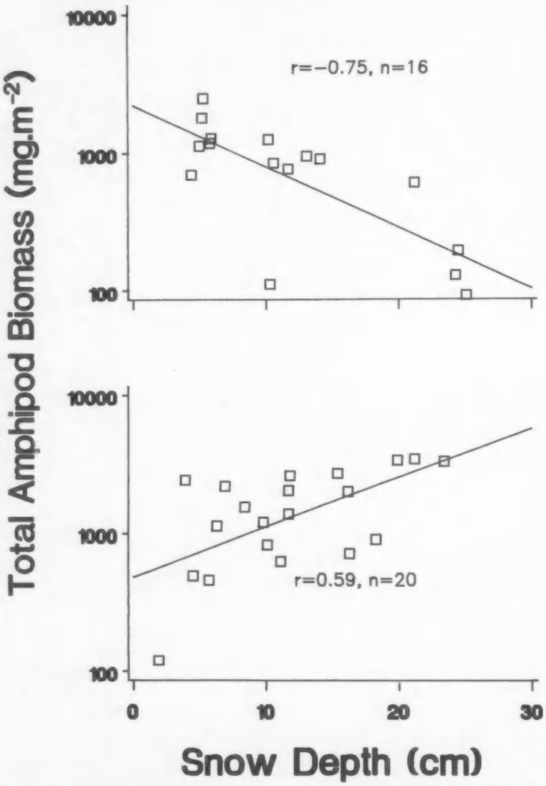

FIG. 9. Relationships between total sub-ice amphipod biomass and snow depth in a 100 × 100 m area as measured on two dates: May 9, 1986 (upper) and May 29, 1986 (lower).

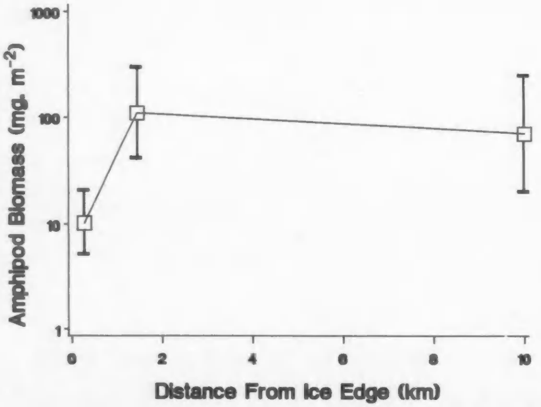

FIG. 10. Change in mean total sub-ice amphipod biomass with distance from the ice-edge in the Griffith Island area (Fig. 4), spring 1986. Data from the last three Resolute area surveys (May 10–June 26) are combined, and mean amphipod biomass is adjusted to the overall mean underlying water depth of 51 m.

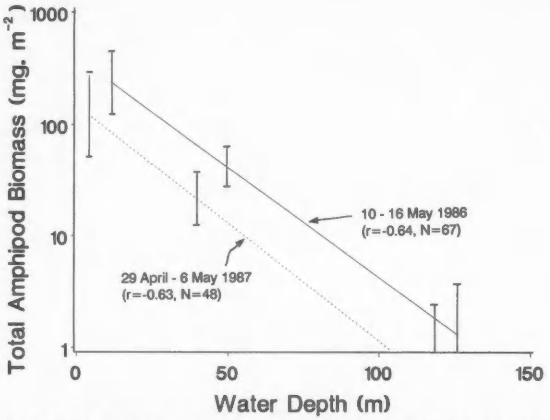

FIG. 11. Regressions between total sub-ice amphipod biomass and water depth from Resolute area surveys, 1986 and 1987. 95% confidence intervals for the mean predicted biomass are shown for the mean, minimum, and maximum water depths.

of 1986. In June, biomass was more evenly distributed over all water depths than at any other time in the spring. In January 1986, biomass was lower and decreased more quickly with increasing underlying water depth than in spring 1985.

The short-term variation experiments in which one station was sampled repeatedly with the camera system showed that significant ($p<0.05$) changes in density occured over a 10-h period (Fig. 12). On June 9 highest densities were observed during the final sampling time between high and low tide. In contrast, highest densities occurred at high and low tide on June 14. Density tended to decrease with increasing current speed (Fig. 13).

Large-scale spatial variations in sub-ice biomass were investigated by applying ANCOVA with depth as a covariate to the remote surveys and the temporally closest Resolute area surveys of 1986. The Wellington Channel and McDougall Sound remote surveys were treated as separate locations, while the survey of April 29 was divided into three locations: western Bathurst Island, Garrett Island, and Lowther Shoal (Fig. 1). Significant differences in the slopes of the water depth against biomass regressions ($p<0.01$) precluded the comparison of biomass levels by ANCOVA. Biomass declined much more quickly with depth at western Bathurst Island and McDougall Sound than in the Resolute area. Sub-ice biomass levels were not significantly different across locations in the 0–50 m depth interval (ANOVA, $p>0.05$) (Table 5).

Species Distributions

Reciprocal averaging was applied to the Resolute area survey data and the Wellington Channel and McDougall Sound remote survey data to determine if gradients in species composition were interpretable as responses to environmental gradients. In all cases, sample scores on the first RA axis showed a strong linear relationship to underlying water depth and distance from shore. The relative species compositions in the 0–30 m, 30–50 m and >50 m depth zones in all 3 yr (Fig. 14) generally substantiated that the sub-ice amphipod species were distributed along a depth or inshore–offshore gradient. In spring 1985 and 1986, *Gammarus setosus* and *Ischyrocerus anguipes* were confined to ice over areas of shallow depth, while *Onisimus litoralis* and *Weyprechtia pinguis* were most abundant over the 30–50 m depth zone. *Apherusa glacialis*, *Onisimus glacialis*, and *Parathemisto* spp. juveniles were most abundant over deeper

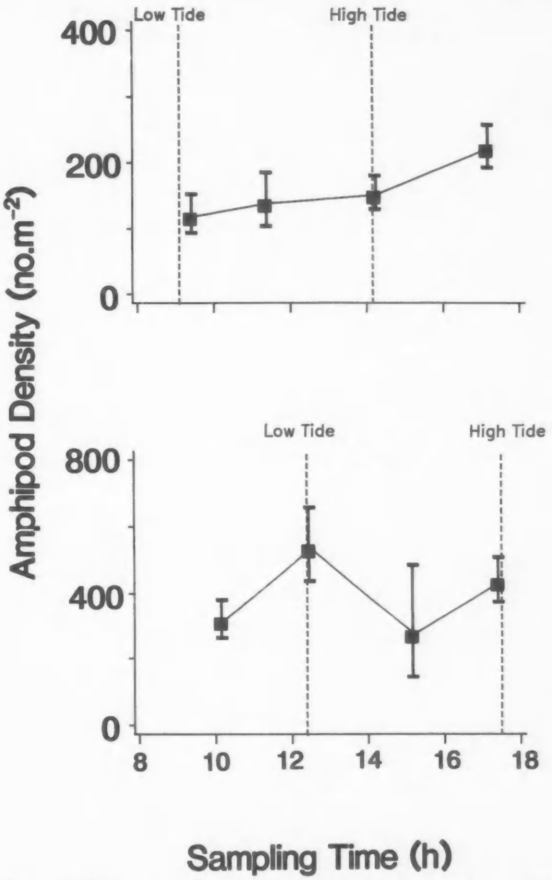

FIG. 12. Change in mean sub-ice amphipod density over a 10-h period at one station as measured on two dates: June 8, 1986 (upper) and June 14, 1986 (lower). Each point is a mean count of 16 video images, and 95% confidence intervals are shown.

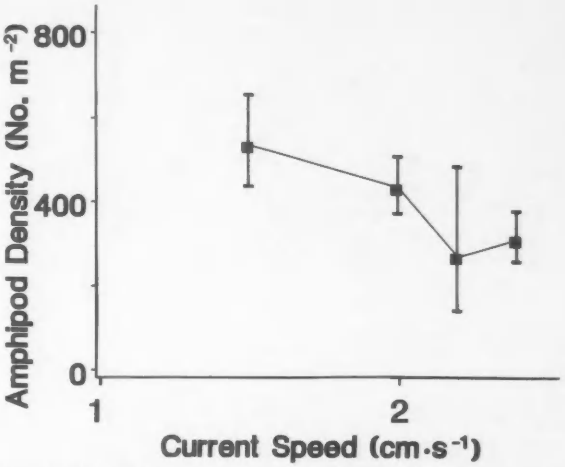

FIG. 13. Change in mean sub-ice amphipod density with current speed at one station over a 10-h period on June 14, 1986. Each point is a mean count of 16 video images, and 95% confidence intervals are shown.

waters. In spring 1987, the fauna could be divided into two groups: an assemblage occurring over shallow waters consisting of *G. setosus*, *I. anguipes*, *W. pinguis*, *O. litoralis*, and *Onisimus* spp. juveniles, and another occurring over deeper waters consisting of *A. glacialis*, *O. glacialis*, and *Parathemisto* spp. juveniles.

Discussion and Conclusions

This study provides the first description of the variation in species composition and total biomass of the sub-ice macrofauna at several spatial and temporal scales. However, many questions remain about the causes of these distributional patterns.

Large Scale Spatial and Temporal Patterns

There were striking variations in species composition both annually (Fig. 7) and over large areas (Fig. 8). Both longitudinal and annual differences reflect alternations in the dominance of *Weyprechtia pinguis*, *Onisimus* spp. juveniles and especially *Onisimus litoralis*. Similarly, annual changes in biomass (Fig. 11) can be explained largely by the great variations in the numbers of *O. litoralis*. No corresponding environmental patterns were found to explain these differences. It is possible that these annual and spatial patterns may be related; i.e. alternations in the year class strengths of *Onisimus* and *W. pinguis* may not be synchronized over large areas. Simultaneous sampling over large areas for several consecutive years would be required to test this hypothesis. The causes of the year class variations themselves remain unknown.

Lowest biomass and species diversity occurred in winter and early spring and increased over the course of the spring until the community disappeared abruptly in mid–late June. This pattern is similar to the seasonal changes observed by other workers (Carey 1982; Cross and Martin 1983). It is probable that these changes are related to the abundance of ice-algae. Ice-algal chlorophyll *a* concentrations increase log-linearly from March to late May at Resolute (H. E. Welch, unpubl. data). Hence, food availability might limit grazer populations early in the spring, but probably not by mid-May when algal concentrations are much higher. The abandonment of the sub-ice habitat coincides with the sloughing-off of the algal layer, and may also be related to changes in ice structure and sub-ice salinity caused by freshwater input from melting ice (Aarset and Aunaas 1987; Percy 1975).

Relationships to Environmental Factors

Underlying water depth was the major correlate of biomass and species distribution of sub-ice macrofauna. Total biomass decreased with increasing water depth at all times and in all areas sampled, and species were distributed along a depth gradient. Sub-ice distribution appears to correspond to the summertime distribution of these species. *Gammarus setosus*, an intertidal species (Thomsen et al. 1986), was most abundant over shallow water. *Onisimus litoralis* and *Weyprechtia pinguis* are intertidal and shallow subtidal species (Cross and Martin 1983; Thomsen et al. 1986) and were most abundant over waters of medium depth. Species found over deep waters (*Apherusa glacialis*, *Onisimus glacialis*, and *Parathemisto* spp. juveniles)

TABLE 5. Mean total sub-ice amphipod biomass in the 0–50 m depth zone at various locations.

Location	Date (1986)	*N*	Mean water depth (m)	Mean biomass ($mg \cdot m^{-2}$)	95% CI[a] ($mg \cdot m^{-2}$)
Western Bathurst Island[b]	19–24 April	9	35	98	18–506
Garrett Island	19–24 April	6	32	9	0–45
Lowther Shoal	19–24 April	3	16	235	24–2269
Wellington Channel	19–24 April	12	26	134	26–705
Resolute Area	19–24 April	31	26	105	46–240
McDougall Sound	10–16 May	12	28	41	5–295
Resolute Area	10–16 May	44	28	141	73—267

[a] CI = confidence interval.
[b] Locations shown in Fig. 8.

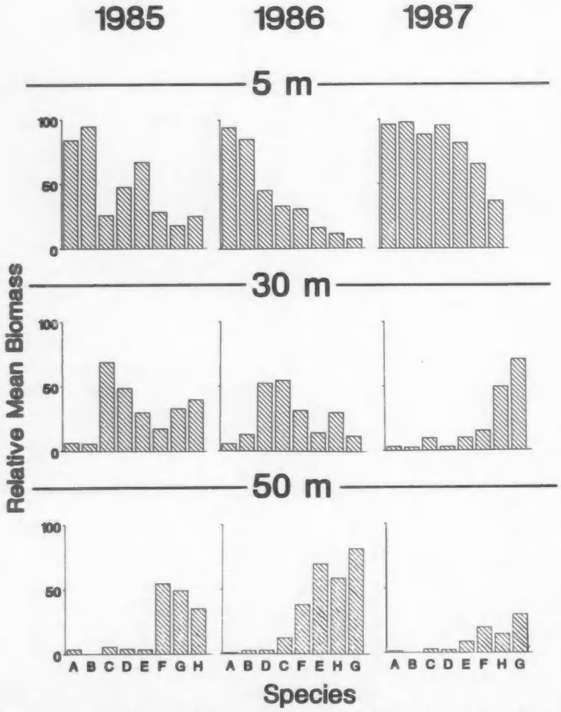

FIG. 14. Mean species biomass in three depth intervals as determined from all spring Resolute area surveys, 1985–87. Biomass levels for each species are adjusted to a common scale (i.e. biomass for each species totals 100 over all depths). Species are ordered from left to right by their mean ranking on the reciprocal averaging axis defining an inshore–offshore gradient. Species A = *Gammarus setosus*, B = *Ischyrocerus anguipes*, C = *Weyprechtia pinguis*, D = *Onisimus litoralis*, E = *Onisimus* spp. juveniles, F = *Apherusa glacialis*, G = *Parathemisto* spp. juveniles, H = *Onisimus glacialis*.

are pelagic during the summer. The largest proportion of the total sub-ice biomass originates from the benthos; hence the relationship between total biomass and water depth.

Gulliksen and Lonne (1987) reported that densities of *Gammarus wilkitzkii* and *A. glacialis* were highest under multi-year ice in perennially ice-covered areas of the Barents Sea. First year ice was apparently colonized from multi-year floes. Multi-year ice is usually rare in the Resolute area, as are the species which were dominant under Barents Sea ice. It appears that both the species composition and the factors affecting macrofaunal distribution in permanently ice-covered, deepwater areas may be different from those found in seasonally ice-covered areas over the continental shelf.

The cause of the apparent depletion of sub-ice macrofaunal biomass near the ice-edge (Fig. 10) remains uncertain. Cross (1982) hypothesized that sub-ice production must be greater in ice-edge areas to support the high densities of animals found there, but could detect no differences in macrofaunal densities corresponding to ice-edge proximity. It is possible that the higher densites of seabirds and seals present in ice-edge areas may lead to a localized cropping of sub-ice macrofauna. The movements of the amphipods themselves may also be a factor; they may periodically drift with the current and "fall off" the ice-edge.

Snow depth was an important correlate of sub-ice biomass at small spatial scales. Total biomass tended to be negatively correlated with snow depth early in the spring, while the opposite was observed later in the spring (Table 4, Fig. 9). Because snow attenuates light, snow depth is the primary determinant of sub-ice algal biomass at Resolute, with algal biomass being a negative logarithmic function of snow depth (H. E. Welch, unpubl. data). Since many sub-ice amphipods consume ice algae (Bradstreet and Cross 1982; Lewis 1987), their distribution is probably related to the abundance of their food source. Simultaneous sampling of macrofauna and sub-ice algae would be necessary to test this hypothesis. Conversely, it should be noted that the decrease of amphipod biomass with increasing depth is opposite the pattern of ice algae, which increase with depth and which are thought to be grazer limited in shallow water (H. E. Welch, unpubl. data).

Diurnal fluctuations in amphipod density may be related to tidal variations in current speed (Figs. 12 and 13). High current speeds may dislodge amphipods from the sub-ice surface or induce them to drift, thus lowering apparent densities. The current speeds of $<2.5\ cm \cdot s^{-1}$ are low compared with speeds up to $60\ cm \cdot s^{-1}$ that occur near Resolute (Cota et al. 1987). Further study on this matter is required, since the time of sampling may influence estimates of sub-ice macrofaunal populations.

Ecological Implications

Water depth was the major influence on both the community structure and total biomass of sub-ice macrofauna. Ice over shallow water (<50 m) is obviously most important in terms of biomass and production. Since extensive areas of shallow water are not common in the eastern Canadian arctic, it seems unlikely that sub-ice macrofauna are of quantitative importance in marine food webs in this area. In other regions, such as the Beaufort Sea and Hudson's Bay, where extensive areas of shallow water do exist, sub-ice macrofauna may be of much greater importance. It is these areas that might be most susceptible to damage by industrial pollution, especially oil spills beneath the ice (Cross and Martin 1983). Such occurrences could directly disrupt the food chain through destruction of the sub-ice community, or contamination of the food chain could render valuable marine resources unusable. The quantitative importance of the sub-ice macrofauna in other areas of the arctic should therefore be investigated.

The observed differences in species composition and total biomass both annually and over large areas might affect the distribution of fish and marine mammals which consume sub-ice macrofauna. Kingsley et al. (1985) observed an east-west gradation in ringed seal densities near Resolute that could not be accounted for by differences in ice type or water depth. Smith and Hammill (1987) noted extreme annual variation in both physical condition and reproductive rates of ringed seals in the western arctic. It is possible that variations in the sub-ice community may be exerting an effect at higher trophic levels.

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Wood Dynamics in Coastal Plain Blackwater Streams[1]

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We quantified woody debris in the river swamps of the sixth order Ogeechee River and several smaller tributaries in the Coastal Plain of the southeastern USA, compared swamp wood with woody debris in the channel, and studied wood movement in the swamp and main channel over 20 mo. Woody debris in the Ogeechee River swamps was relatively low (0.362–0.880 kg ash-free dry mass (AFDM)/m^2) in comparison to several mixed temperate deciduous forests. Similarly, wood in the tributary swamps was low (mean = 0.82 kg AFDM/m^2), and there were no trends along the river continuum. Wood in the channels of both the Ogeechee (6.46 kg AFDM/m^2) and a fourth order tributary (2.24 kg AFDM/m^2) were significantly higher than found in their adjacent floodplains. Woody debris appeared to increase in stream channels from smaller tributaries to the sixth order river, opposite of that observed in other river systems. Tagging of logs showed that only 17% of wood in the Ogeechee channel had moved after 3 major floods, much less than in the swamps (21–84%). The abundance and stability of woody debris in the main channel allows it to be a major habitat type and source of food for both riverine invertebrates and fishes. The fate of most swamp wood appears to be decomposition and fragmentation, rather than import to the river channel.

Les auteurs ont quantifié les débris ligneux dans les marécages de la rivière de sixième ordre Ogeechee et de plusieurs petits tributaires de la plaine côtière du sud-est des États-Unis; ils ont également comparé le bois de marais aux débris ligneux trouvés dans le chenal et étudié le déplacement du bois dans le marais et le chenal principal pendant 20 mo. Les débris ligneux trouvés dans les marais de la rivière Ogeechee sont relativement peu abondants (0.362–0.880 kg AFDM (masse sèche sans cendre)/m^2) comparativement à ceux de plusieurs autres forêts de feuillus mixtes des climats tempérés. De la même façon, le bois trouvé dans les marécages des tributaires était peu abondant (moyenne = 0.82 kg AFDM/m^2) et aucune tendance n'a pu être dégagée le long de la rivière. Le bois trouvé dans les chenaux de la rivière Ogeechee (6.46 kg AFDM/m^2) et d'un tributaire de quatrième ordre (2.24 kg AFDM/m^2) était beaucoup plus abondant que dans leurs plaines inondables adjacentes. Les débris ligneux semblaient augmenter dans les chenaux des cours d'eau depuis les petits tributaires jusqu'à la rivière de sixième ordre, ce qui contredit ce qui est observé dans les autres bassins hydrographiques. L'étiquetage de billes de bois a révélé que seul 17 % du bois du chenal de la rivière Ogeechee s'étaient déplacés après trois crues importantes, ce qui est beaucoup moins que dans les marécages (21–84 %). À cause de l'abondance et de la stabilité des débris ligneux qui s'y trouvent, le chenal principal constitue un type d'habitat important et une précieuse source de nourriture pour les invertébrés riverains et les poissons. Le bois des marécages finit probablement par se décomposer et par se fragmenter au lieu de se déplacer dans le chenal de la rivière.

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The importance of allochthonous organic matter to the functioning of stream ecosystems has been well recognized for at least 25 yr (Nelson and Scott 1962; Hynes 1963), but only in the last decade has wood been identified as a critical structural component (e.g. Marzolf 1978; Bilby and Likens 1980; Triska and Cromack 1980). Descriptions of streams along the continuum from small tributaries to large rivers generally emphasize the role of wood in the smaller systems (orders 1–4), with wood becoming of negligible importance in orders 5 or higher (e.g. Minshall et al. 1983; Naiman et al. 1986, 1987). Presumably, stream power, a measure of the stream's ability to perform work (Leopold et al. 1964), is sufficient to scour most wood from larger systems, particularly those with relatively high gradients (e.g. Wallace and Benke 1984; Bisson et al. 1987). However, historical accounts suggest that anthropogenic manipulations are sometimes responsible for the small amount of wood currently found in large rivers (McCall 1988; Sedell and Froggatt 1984; Triska 1984).

Low-gradient streams appear to differ markedly in many ecological characteristics from these high-gradient systems, including the quantities and role of woody debris. For example, we have found that wood in the sixth order Ogeechee River (Coastal Plain of the southeastern USA) is comparable in magnitude with wood found in some low-order, high-gradient streams (Wallace and Benke 1984). Another obvious distinction is that these low gradient streams have broad floodplain forests

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(swamps) that are often inundated for several months per year. Wood on the forest floor may be as much in contact with stream water over a year as the large amounts of downed wood which hang above smaller streams, such as in the Cascades of the Pacific northwestern USA (Sedell et al. 1988).

The role of wood in flowing waters has been discussed by many authors, and extensively reviewed by Harmon et al. (1986). In forested headwater streams of low order, wood serves as a retention device for allochthonous organic material and strongly affects nutrient dynamics. As a major structural feature of streams, wood also provides a variety of habitat types for all organisms, but particularly invertebrates and fishes. In the low-gradient, sandy-bottom streams of the southeastern USA, the importance of wood as a major habitat has now been documented in streams of several sizes (Cudney and Wallace 1980; Benke et al. 1984; Wallace and Benke 1984; Smock et al. 1985; Thorp et al. 1985). High secondary production on woody substrates is an important source of food for many insectivorous fishes (Benke et al. 1985).

In a series of studies on the Ogeechee River, we have stressed the importance of both organic debris (including wood) and river–floodplain interactions. Specifically, these studies have examined decomposition and movement (Cuffney and Wallace 1987; Cuffney 1988), hydrodynamic properties at different flood stages (Pernik and Roberts 1985; Roberts et al. 1985), the role of dissolved organic matter and bacteria in total system metabolism (Meyer 1986; Edwards 1987; Edwards and Meyer 1987), and synthesis of the storage and transport of organic matter (Benke and Meyer 1988). In view of the importance of wood and the interaction between river and floodplain, we have undertaken additional studies to examine woody debris in floodplain swamps and to examine its stability and mobility in both channel and swamp.

Our major objectives were to (1) quantify woody debris in two Ogeechee River swamps for comparison with other forest types and with the high values obtained in the main Ogeechee channel, (2) quantify woody debris in the swamps of several smaller tributaries of the Ogeechee River for comparison with the main stem swamp, and (3) determine the stability of woody debris in both the main channel and swamp by analysis of its movement and disappearance. Each of these objectives has relevance regarding organic matter budgets and the significance of wood as habitat for aquatic animals.

Study Site

Our main study site at an elevation of 6.1 m a.s.l. is on the sixth order Ogeechee about 63 river km from the mouth (for full description, see Wallace and Benke (1984); Benke and Meyer (1988)). Stream gradient here is only 19.6 cm/km as the river meanders within a heavily forested floodplain swamp that is often >1 km in width. Mean annual discharge is 65.5 m^3/s (United States Geological Survey 1987), but when the river exceeds 125 m^3/s the floodplain is completely inundated (Fig. 1). Because moderate inundation of the floodplain swamp occurs even at average discharge, we refer to 100% inundation (125 m^3/s) as a major flood. Extensive flooding is a frequent and extended event with a 200 m^3/s flood having a return period of about 1 yr (Pernik and Roberts 1985). The largest flood during our wood movement measurements (300 m^3/s, Fig. 1) had a return period of about 1.7 yr. While a flood frequency curve for the Ogeechee (Pernik and Roberts 1985) predicts a flood of 750 m^3/s to have a 10-yr return period, only one flood of this magnitude has occurred since the U.S. Geological Survey started gaging the river 50 yr ago. The largest flood during our studies from 1981 through 1988 was about 350 m^3/s.

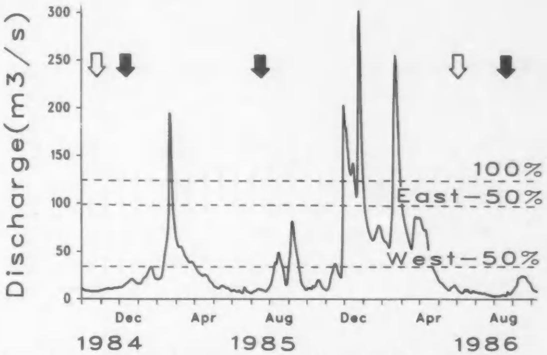

FIG. 1. Discharge and sampling times during period of wood movement study in the Ogeechee River (from U.S. Geological Survey 1986, 1987). Open arrows indicate initial and final sampling times in the main channel. Solid arrows indicate marking and sampling times of wood in the Ogeechee River swamps. Horizontal dashed lines indicate the 50 and 100% inundation level of the East Swamp and the West Swamp.

An interesting hydrodynamic characteristic of this river, and perhaps Coastal Plain rivers in general, is that average stream velocity increases (up to about 0.6 m/s) with discharge until approximately 100% inundation (Roberts et al. 1985). At this point, the floodplain carries only about 13% of total discharge. Beyond this, velocity rapidly declines to about 0.3 m/s and remains low until discharge reaches about 250 m^3/s at which time about 50% of discharge flows through the floodplain. At greater discharge, average velocity gradually increases again, but not beyond the maximum reached at 125 m^3/s (Roberts et al. 1985).

Methods

To quantify the amount of woody debris found in the Ogeechee floodplain, we used site locations established by Cuffney (1984, 1988) in an earlier study of swamp organic matter dynamics. There were five sites on both the east side of the river (swamp width = 1.0 km) and the west side (swamp width = 200 m). Within each swamp, sites were equally separated from one another, beginning near the river bank and extending to the edge of each swamp. At each site, we established four 30-m transects on 11–12 December 1984, beginning at one of Cuffney's original markers. This transect length was similar to those used in the river (Wallace and Benke 1984). The compass direction of each transect was determined by a random number generator. Any compass headings within 20 degrees of each other at each site were considered to be duplicates, and a substitute heading was selected. We measured the diameter of all downed woody debris intersected by the vertical plane along each transect line. These measurements were used to estimate wood surface area and volume with the line intersect technique described by Wallace and Benke (1984).

During the summer of 1986, we used the line intersect technique to measure wood in the channel and floodplain of Black Creek, a fourth order tributary of the Ogeechee (10 transects each). This site was located near the Rt 280 bridge, approximately 10 km upstream of our earlier measurement of channel wood on Black Creek, nearer its mouth on the Ogeechee River (see full description in Wallace and Benke (1984)). Transect length in the channel depended on channel width and averaged 8.6 m (range 6–11). Transect length in the swamp was 20 m. We also measured wood in the floodplain swamps of two smaller tributaries: Ash Branch, a third order stream in the lower Coastal Plain (two sites); and Cowpen Creek, a third order stream in the upper Coastal Plain (two sites). At each of the smaller tributaries, we measured 10 transects of 10 m length (we used a shorter transect length due to narrower floodplains). We did not attempt to measure channel wood in these third order tributaries because channel boundaries were very arbitrary in smaller systems, particularly Ash Branch. In fact, quantification of the tributary wood was conducted during a major drought and Ash Branch was completely dry. There was no noticeable difference in wood quantities between the swamp and apparent channel area.

Ash-free dry mass (AFDM) of wood was estimated as the product of volume and specific gravity. Wallace and Benke (1984) estimated specific gravity (grams AFDM per cubic centimetre) of wood in the main channel of the Ogeechee and Black Creek. We followed a similar procedure for wood in the floodplain. Thirty core samples were taken from logs using an increment borer (5.5 mm internal diam.), and 10 small sticks (ca. 20 mm diam.) were also collected. Samples were evenly divided between east and west swamps.

Movement of woody debris in the main channel of the Ogeechee River was estimated by establishing 10 permanent transects (using eyebolts attached to trees on the bank as our transect anchors) on 25–27 October 1984, a period of very low discharge (Fig. 1). For each transect, a line marked at 1 m intervals was stretched across the river. The diameter of all wood intersected by a vertical plane defined by the transect line was measured, including wood below water (which averaged 87.9 ± 5.4 (SE) cm in depth) and up to 2 m above the water surface. In an earlier study (Wallace and Benke 1984), we established that $<1\%$ of total wood volume was found in stems <1 cm; therefore, we measured only stems >1 cm diameter. The volume, AFDM, and habitat surface area were estimated using the equations presented in Wallace and Benke (1984). These measurements established our baseline quantities.

During the above sampling, we marked as many stems as possible at each transect with 3-cm diameter aluminum tags nailed into the wood. Not all measured wood could be marked due to small size (<5 cm stems) or location (access to submerged stems was sometimes difficult). We repeated our quantification of these transects during a period of low discharge on 29–30 May 1986, after 19 months and three major floods (Fig. 1). Because we had permanent transects and knew the precise location of each marked piece of wood, we could determine whether marked wood moved more than 1 m. In most cases, if the wood had moved, it had moved too far to be relocated, and we present our results as percentage of wood stems moved. Our combination of wood quantification and wood marking enabled us to compare transect totals after 19 months, as well as movement of individual stems.

Cuffney (1988) measured the movement of leaf and woody litter (1–3 cm diameter) in the Ogeechee swamps, but he did not measure movement of larger wood. In the present study, we concentrated on movement of "large" wood in the Ogeechee River swamp, marking five logs (4–24 cm diameter) with an aluminum tag at each of the five sites in both east and west swamps on 11–12 December 1984 (Fig. 1). Thus, 25 logs were marked in each swamp and their location was recorded by distance and compass setting from the center of a marker. We attempted to relocate all marked logs on 18 July 1985 (after one major flood) and 23 August 1986 (after two additional floods) (Fig. 1). Wood could usually be relocated and its position and direction measured.

Results

Wood Quantification in Ogeechee River Floodplain

Specific gravity of wood in the Ogeechee floodplain (0.332 ± 0.015 g AFDM/cm^3, ± 1 SE, $n = 40$) was significantly less than wood in the main channel (0.408 ± 0.028, $n = 50$). No significant differences were found between East and West Swamps, nor between small sticks and cores from logs. Mean percent ash for wood samples in the swamp was $2.133 \pm 0.34\%$. The mean specific gravity from the Ogeechee floodplain was applied in calculating wood AFDM in all floodplains.

Several hundred stems were measured along each transect in both the West and East Swamps (420–765 stems per site). Stem density was higher ($p<0.05$) in the East Swamp, but larger stem diameters ($p<0.05$) were found in the West Swamp (Table 1). The larger stem diameters resulted in higher wood volume and mass ($p<0.05$) in the West Swamp. However, the absolute differences in these statistics among swamps were relatively small. Furthermore, wood surface areas were not significantly different between swamps. All wood statistics from both swamps (except for stem density) were lower ($p<0.05$) than wood from the main channel (Table 1). In the case of wood mass, these differences were quite large (0.880 and 0.362 in the swamps versus 6.46 kg AFDM/m^2 in the channel; Wallace and Benke 1984).

Wood Quantification in Floodplains of Ogeechee Tributaries

Mass of wood and mean stem diameter in floodplains of the smaller tributaries (excluding Black Creek) were very similar (Table 2) with no significant differences among the four third order sites (Anova, and Tukey's multiple comparison test, $p>0.05$). While there were differences in stem density (number per metre) among swamps (Anova, $p<0.01$), it was not of sufficient magnitude to cause significant differences in wood mass. The fourth order Black Creek Swamp had the lowest stem density of all tributaries, and this contributed, in part, to significantly lower wood volume and mass (Table 2). Mean wood mass for all five tributaries, including Black Creek (0.82 kg AFDM/m^2) was somewhat higher than the mean mass for the Ogeechee River swamps (0.62 kg AFDM/m^2), but the difference was not significant. In summary, there does not appear to be a trend in the amount of woody debris found in swamps along the Ogeechee River continuum.

Wood mass was higher ($p<0.05$) in the Black Creek channel (2.24 kg AFDM/m^2) than in the swamp (0.365 kg AFDM/m^2) due to a significantly higher mean stem diameter in the channel (Table 2). However, channel wood mass was lower than that found in the same channel 10 km downstream (4.98 kg AFDM/m^2), which was lower than that found in the Ogeechee (6.46 kg AFDM/m^2; Wallace and Benke 1984). Only the upstream Black Creek channel and Ogeechee channel were significantly different (Tukey's HSD multiple comparison test, $p<0.05$) due to considerable variability in all channels.

TABLE 1. Woody debris in two swamps on the Ogeechee River (East and West), with five separate sites in each swamp and four transect lines at each site. Channel means are from Wallace and Benke (1984) and J.B. Wallace (unpubl. data).

Site	Square metre wood surface per square metre ground	Wood volume (m^3/m^2)	Wood mass (kg AFDM/m^2)	Mean stem diameter (cm)	Stem density (No./m)
West Swamp					
Site 1	0.234	0.00588	1.952	1.10	4.65
2	0.158	0.00093	0.309	0.83	3.79
3	0.150	0.00122	0.405	0.85	3.50
4	0.234	0.00237	0.787	1.06	4.54
5	0.229	0.00280	0.930	1.08	4.72
Mean	0.201	0.00265[a]	0.880[a]	0.98[a]	4.24[a]
East Swamp					
Site 1	0.212	0.00096	0.319	0.74	6.15
2	0.273	0.00142	0.471	0.87	6.37
3	0.156	0.00057	0.189	0.74	4.41
4	0.220	0.00094	0.312	0.77	5.88
5	0.247	0.00158	0.525	0.89	5.59
Mean	0.222	0.00109[a]	0.362[a]	0.80[a]	5.68[a]
Channel	0.433[b]	0.0148[b]	6.46[b]	2.29[b]	4.16[c]

[a] Means are different ($p < 0.05$) between East and West swamps.

[b] Channel means are different ($p < 0.05$) than swamp means.

[c] Channel mean is different ($p < 0.05$) than East swamp mean.

TABLE 2. Woody debris in floodplains of five Ogeechee River tributaries (two in upper Coastal Plain, three in lower Coastal Plain). All values are based on 10 transects from each floodplain. Also included are estimates of wood from the main channel of the largest tributary (Black Creek).

	Wood volume (m^3/m^2)	Wood mass (kg AFDM/m^2)	Mean stem diameter (cm)	Stem density (No./m)
Upper Cowpen	0.00247	0.82	1.05	3.98[c]
Lower Cowpen	0.00298	0.99	0.93	5.78[c]
Ash Branch A	0.00306	1.02	0.91	8.47[c]
Ash Branch B	0.00283	0.91	0.97	6.92[c]
Black Creek Swamp	0.00110[a]	0.37[a]	1.01	3.59[c]
Black Creek Channel	0.00556[b]	2.24[b]	1.94[d]	3.88

[a] Wood volume and mass less ($p < 0.05$) in Black Creek Swamp than tributary floodplains.

[b] Wood volume and mass higher ($p < 0.05$) in Black Creek channel than in Black Creek Swamp.

[c] Differences in stem density significant ($p < 0.01$) among all floodplains.

[d] Mean stem diameter higher ($p < 0.01$) in Black Creek channel than in Black Creek Swamp.

Wood Movement in Ogeechee Swamp

Most of the 25 logs tagged in both the East and West Swamps in December 1984 were recovered in both July 1985 (92–96%) and August 1986 (80–88%) (Table 3). Much more wood moved in the West Swamp than in the East Swamp, and the percentages were consistent from one year to the next. In the low-lying West Swamp, 83–84% of the wood moved each year, but in the higher East Swamp, only 21–28% of the wood moved. Furthermore, of the wood that moved, it moved greater distances in the West Swamp than the East (Table 3 and Fig. 2). Note that in Fig. 2, the center of the vectors in both the swamps does not imply that all wood was released at these exact points. Marked wood was actually distributed across the entire width of each floodplain in the general vicinity of the vector centers. Although there was considerable scatter in almost all directions (Fig. 2), the net movement of wood in the West Swamp was consistently in the direction of the main channel flow (resultant vector was 193–203 degrees). Direction of wood movement in the east swamp (135–253 degrees) was generally downstream, but was less consistent than in the west swamp.

TABLE 3. Wood movement experiment in two Ogeechee River floodplains (East and West). Wood tagged on 11–12 December 1984 and recovered on 18 July 1985 and 23 August 1986 (See Fig. 2a).

	Logs marked	Logs recovered	No. (%) moved[a]	Mean distance moved (m)[b]	Heading (degrees) resultant vector[b]
East Swamp					
1985	25	24	7(28)%	2.5	256
1986	24	22	5(21%)	2.2	135
West Swamp					
1985	25	23	21(84%)	6.8	203
1986	23	20	19(83%)	8.6	193

[a] Includes logs not relocated.

[b] Includes only those logs that moved and were relocated.

Wood Movement in Ogeechee Channel

A total of 83 logs of various sizes were tagged along 10 fixed transects in October 1984. On 29 May 1986, after three major floods, we attempted to relocate all marked wood at each transect. Unfortunately, reference marks for one of the transects could not be relocated; thus, calculations are based on only nine transects (with 78 tagged logs). Approximately 17% (with a range 0–30% among the transects) of the logs had moved (i.e. disappeared) (Table 4). The highest percentage of logs was lost in the <10 cm diameter category (42%). For logs >10 cm,

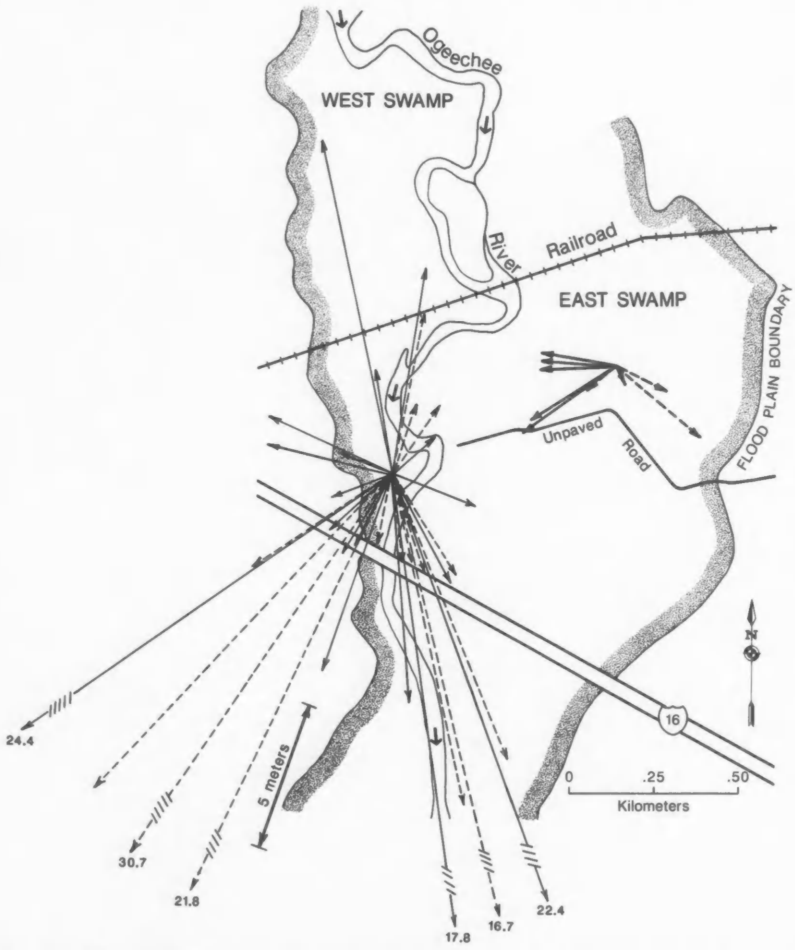

FIG. 2. Direction of wood movement in the West and East Swamps of the Ogeechee River. Logs were tagged in December 1984 and relocated in July 1985 (solid vectors) and August 1986 (dashed vectors). The length scales of the map and vectors differ by about 100×.

TABLE 4. Movement of marked wood (snags) in the Ogeechee River channel from 25 October 1984 to 29 May 1986.

Size class diameter (cm)	Number of logs	Number moved	Percent moved
5–10	12	5	42
10–20	31	5	16
20–30	14	2	14
30–40	10	1	10
>40	11	0	0
Total	78	13	17

only 12% had moved, with the percentage declining as log size increased (Table 4). There was no trend in percent lost between transects along bends versus straight stretches of the river in any size class.

Wood movement data present an interesting contrast to the measure of change of wood volume in the transects. Total wood volumes increased in seven out of nine transects from 1984 to 1986 (Fig. 3a), with a net increase in volume across all transects of 8.6% (Table 5). The greatest increase in volume (70%) was for wood with a diameter <10 cm, although this size class composed only 4% of total wood volume (Table 5). There was a similar increase in surface area (Table 5). The numbers of stems also increased in seven out of nine transects (Fig. 3b), with the greatest increase due to those <10 cm (Table 5). It is apparent from Fig. 3b that the large increases in number of stems in transects 2 and 6 are due to new wood being imported into those transects. Furthermore, the smaller increases in transects 3, 4, 5, 7, and 9 are also probably real increases (rather than sampling error). While small changes in estimated wood volume (Fig. 3a) could be due to errors in measuring diameter, the numerical increases (Fig. 3b) suggest that the net accumulation of wood (both numbers and volume) is a real phenomenon. Thus, even though wood was lost from each transect as shown in our tagging experiment, imported wood more than made up for these losses in seven out of nine cases.

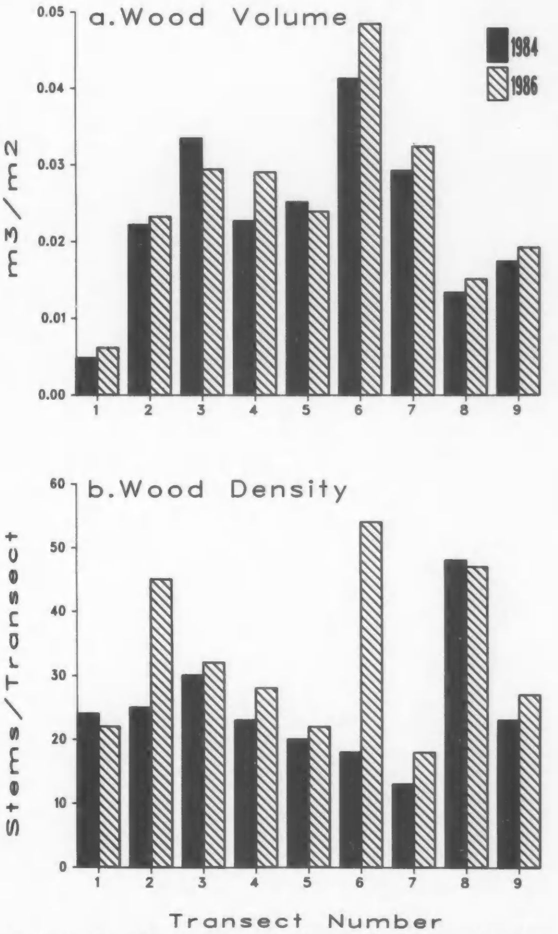

FIG. 3. (a) Quantification of wood volume (m^3/m^2) along nine fixed transects in the Ogeechee River from 25 October 1984 to 29 May 1986. (b) Number of stems measured along the same nine transects in 1984 and 1986. Total initial number of stems = 224.

Using information from the marked wood experiment (Table 4) and the comparison of fixed transects between dates (Table 5), we can make a rough approximation of the percentage of wood found in 1986 that was imported over the previous 19-mo period. For the 1–10 cm size class, 42% of marked stems were lost, but the total number increased by 37%. Therefore, about 79% of the stems in this small size category were new. For the larger size classes (>10 cm), 12% of marked stems were lost, and the total number increased by 11%. Thus, about 23% of the stems >10 cm diameter were new after 19 mo.

Discussion

Dynamics of Wood Debris in Mainstem Channel

Wood mass in our Coastal Plain streams is considerably higher than has been demonstrated for other sixth order streams from high gradient catchments. The greatest amount of channel wood originates from large trees which fall into the river as banks are undercut, and thus most wood accumulates along the erosional bank (see figure 2 in Wallace and Benke 1984). The boles are also the most stable; none of the marked stems >40 cm moved during our study (Table 4). During the periods of moderate flooding (<300 m^3/s) observed during our study, the floodplain buffers stream velocity (Roberts et al. 1985) and probably inhibits movements of large woody debris. At extremely high discharge (>400 m^3/s), stream velocity and power may increase sufficiently to dislodge some of the accumulations. However, long-term measurements on the order of decades are required to assess the impact of extreme flooding on inputs of whole trees and their movement within the main channel.

Transient wood from upstream areas, broken branches from bankside trees, or wood from the swamp may enhance the total amount of wood in debris accumulations. During periods of moderate flooding (Fig. 1), there was a net increase of woody debris (surface area, volume, number of stems) at fixed transects in the main channel of the Ogeechee (Table 5). Small wood (<10 cm) displayed the greatest turnover and accumulation (Tables 4 and 5). Based on the rate of accumulation measured over 19 mo (Table 5), wood surface area would double about every 5.3 yr and volume would double every 13.3 yr. Over the long term, such extrapolation would lead to an extremely large mass of wood in the Ogeechee channel, even without input of new trees. Whether extremely high discharge would reverse this trend through a reduction of woody debris is unknown, but the history of snagging operations in many low-gradient rivers of the USA attests to the fact that snag accumulations can be substantially higher than we have measured (e.g. Sedell and Froggatt 1984; Triska 1984; McCall 1988).

Stability of wood in the Ogeechee is similar to that of the heavy debris accumulations found in low-to-middle order Cascade streams where large pieces (>10 cm diam.) have biomass turnover times of 12 to 83 yr (Lienkaemper and Swanson 1987). In contrast to the lateral undercutting of bankside trees found in the Ogeechee, wood in Cascade streams is primarily delivered from the steep slope above the bank, apparently blown down by wind (Lienkaemper and Swanson 1987).

Unlike the heavy debris accumulations which hang suspended above low-order streams in high gradient catchments for much of the year (e.g. Sedell et al. 1987), most wood in the Ogeechee River channel is inundated throughout the year (Wallace and Benke 1984). This is significant from the viewpoint of aquatic invertebrates because many species are found exclusively on woody debris (or snags). Depending on river height, the snag habitat can represent 20 to 50% as much surface area as the total benthic area. The stability of the snag habitat is apparently what makes it so attractive for invertebrate colonization as biomass and production can be very high (Wallace and Benke 1984; Benke et al. 1984; Benke and Meyer 1988). Small stems <10 cm diameter are the least stable size class, but their average longevity (>2 yr) is far longer than the life span of most Ogeechee River invertebrates. The major instability associated with the habitat is that the upper portions are subject to desiccation with the rise and fall of the river (see Fig. 3 in Wallace and Benke 1984).

Quantity and Dynamics of Floodplain Woody Debris

The estimates of mass of woody debris on forested floodplains of the Ogeechee River (Table 1) and its tributaries (Table 2) are skewed toward the low end of the ranges reported for

TABLE 5. Mean surface area, volume, and number of stems per transect (9 transects) for woody debris in the Ogeechee River on 25 October 1984 and 29 May 1986. The mean absolute increase and the mean percentage increase between the two dates are given.

	Wood diameter (cm)	1984	1986	Mean absolute increase	Mean percentage increase
Surface area (m^2/m^2)	1–10	0.081	0.131	0.050	61.7%
	>10	0.287	0.322	0.035	12.2
	Total	0.368	0.453	0.085	23.1
Volume (m^2/m^2)	1–10	0.0010	0.0017	0.0007	70.0
	>10	0.0223	0.0235	0.0012	5.4
	Total	0.0232	0.0252	0.0020	8.6
Number of stems per transect	1–10	16.6	22.8	6.2	37.3
	>10	8.4	9.3	0.9	10.7
	Total	24.9	32.1	7.2	28.9

several mixed deciduous forests (Triska and Cromack 1980; Harmon et al. 1986). Conversely, the productivity of these swamp forests is quite high, as litter fall in the Ogeechee floodplain is in the upper range of values for temperate deciduous forests (Cuffney 1988). This apparent discrepancy may be attributed to: (1) wood being eventually washed out of the swamps, and (2) rapid decomposition and fragmentation that likely occurs in this warm, humid environment.

In contrast to snags in the main channel, woody debris in swamps is very unstable. During floods, swamp wood tends to float, and does not provide the same stable habitat for invertebrates as that in the main channel. The primary direction of wood movement in both floodplains was downstream and toward the main river channel, although between-swamp differences were observed (Fig. 2, Table 3). The relatively high rates of flow through the West Swamp (Fig. 1) undoubtedly contribute to the much greater rate and distance moved by woody debris here in comparison to the East Swamp. For example, at discharges of 226 m^3/s, 43% of the total discharge of the Ogeechee River flows through the low-lying West Swamp (Pernik and Roberts 1985). Wood movement in the West Swamp (>80% moved, Table 3) greatly exceeded that of the main stream channel of the Ogeechee where only 17% moved (Table 4) over a 19-mo period which encompassed three floods (Fig. 1). In fact, even wood movement in the higher East Swamp (>20% moved, Table 3), which had relatively low flow during our study period, exceeded that of the main stream channel. As swamp wood moves in a downstream direction, some of the wood will eventually enter the river channel, even during moderate floods. However, greater amounts of wood may be exported from swamp to river during floods greater than those observed during our period of study.

Patterns of Woody Debris along the River Continuum

No trends were evident in the quantity of floodplain wood from small tributaries to the sixth order Ogeechee. Thus, there is no evidence suggesting that the factors operating on the inputs and losses of swamp wood depends on size of stream.

In contrast to wood in the swamp, channel wood appeared to increase along the river continuum in these low-gradient streams. Channel wood in third order tributaries appeared similar to that found in their floodplains (i.e. <1 kg AFDM/m^2). Channel wood increased in fourth order Black Creek from 2.24 kg/m^2 to 4.98 kg/m^2 downstream, and to 6.46 kg/m^2 in the sixth order Ogeechee River. Although this increase is not extremely dramatic, it is just the opposite of that observed in high gradient systems (Minshall et al. 1983; Naiman et al. 1986, 1987). These divergent trends are probably attributable to the major differences in geomorphology between low and high gradient systems. Even sixth order Coastal Plain rivers such as the Ogeechee do not seem to have the power to move wood from the channel as occurs in high gradient systems like the McKenzie (Triska and Cromack 1980; Minshall et al. 1983); hence, the apparent downstream increase in channel wood.

Role of Wood in Organic Matter Budgets of Coastal Plain Streams

Benke and Meyer (1988) have shown that woody debris is an important fraction of total organic matter in the swamps and main channel of the Ogeechee River. Wood comprises roughly 12% of total organic matter in the swamps (83% in soil and 5% in leaf litter; also see Cuffney 1988), and 70% of the total in the main channel (21% fine particulate organic matter (FPOM) and 9% leaf coarse particulate organic matter (CPOM). Although the swamp contains less wood per unit area, the mean swamp width is about 40 times greater than channel width (1340 versus 33 m over an extended distance, Cuffney 1984; Benke and Meyer 1988); hence, the swamp contains a greater absolute mass of woody debris than the channel (832 kg/m of stream length versus 213 kg/m).

Wallace and Benke (1984) suggested that there is a net movement of wood from swamp to channel during floods which is partially responsible for the larger accumulations of wood in the channel. Our present analyses suggest that while some transient wood in the channel may have been flushed from the swamp, the net loss is likely to be small and insufficient to account for these differences. If we assume the mean distance of wood (>4 cm diameter) moved is 3.5 m/yr (Table 3), and the average travel distance for wood through the swamp is 350 m (a conservative estimate), then about 1% of the wood will leave the swamp per year. This implies that it will take the average piece of wood 100 yr before it leaves the swamp. Since wood decomposition rates at the terrestrial/aquatic interface are likely to be high (Triska and Cromack 1980; Sedell et al. 1987), we predict that physical and biological fragmentation will transform most wood into dissolved organic matter (DOM) and FPOM before it can leave the swamp as intact logs. The lower specific gravity and greater state of decomposition for wood in the swamp supports this interpretation. The overriding role of decomposition is most likely to predominate in larger and higher-elevation swamps (e.g. East Swamp) where total travel distance is greater and distance actually moved less than in low-lying, narrow swamps (e.g. West Swamp). In contrast to the transport of wood >4 cm diameter, Cuffney (1988) estimated that 8.3–28.7% of the leaf litter and small wood (<3 cm diameter) is flushed from the swamps to the channel annually.

In summary, channel wood in the Ogeechee River plays its major role as a structural feature and is important as a major habitat type for invertebrates and fishes. Unlike high gradient streams, wood in Coastal Plain streams is at least as important in its lower reaches as it is upstream. Swamp wood accumulations are low in comparison to most temperate forests, apparently due to rapid decomposition rates. Swamp wood plays less of a structural role than channel wood, but probably represents a major source of DOM and FPOM to the river. Clearly, woody debris can be extremely important in many types of lotic systems, but basin geomorphology will determine its particular role in each system.

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Cascading Effects of Decreased Salinity on the Plankton, Chemistry, and Physics of the Great Salt Lake (Utah)

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Wurtsbaugh, W. A., and T. Smith Berry. 1990. Cascading effects of decreased salinity on the plankton, chemistry, and physics of the Great Salt Lake (Utah). Can. J. Fish. Aquat. Sci. 47: 100–109.

Physical, chemical and biological variables were measured in the Great Salt Lake during 1985–87, when salinity in the mixolimnion was near 50 g/L, much lower than the 250 g/L maxima recorded in 1963. Decreased salinity has been accompanied by a change in macrozooplankton from one species (*Artemia franciscana*), to an assemblage with one rotifer, two copepods, *Artemia*, and the corixid *Trichocorixa verticalis*. Predation by the corixid may now limit *Artemia* to low densities ($<100 \cdot m^{-3}$). The low biomass of *Artemia* and other zooplankton has reduced grazing pressure on the algal community so that high chlorophyll levels (5–44 $mg \cdot m^{-3}$) and low Secchi depths (0.8–2.7 m) are now present throughout the year. The algae presently reduce soluble reactive phosphorus and inorganic nitrogen in the mixolimnion to below 5 and 50 $\mu g \cdot L^{-1}$, respectively. Shading in the 7-m thick mixolimnion by algae, and by purple-sulfur bacteria in the chemocline, decreases light penetration so that the monimolimnion now maintains a nearly constant temperature (9–11°C) throughout the year. The data support the hypothesis that the effects of corixid predation have cascaded through the Great Salt Lake, affecting herbivores, nutrients and thermal stratification.

Des variables physiques, chimiques et biologiques ont été mesurées dans la zone pélagique du Grand Lac Salé au cours de la période 1985–87, alors que la salinité dans le mixolimnion atteignait presque 50 $g \cdot L^{-1}$ (salinité maximale mesurée : 250 $g \cdot L^{-1}$, en 1963). Le bassin peu profond (12 m) situé au sud du lac est méromictique : cela s'explique par l'écoulement par densité d'eaux saumâtres provenant du bassin nord dont les eaux sont plus salées. La diminution de la salinité dans le bassin sud s'est accompagnée d'une modification dans la composition du macrozooplancton qui est passé d'une seule espèce (*Artemia franciscana*) à un ensemble d'espèces comprenant un rotifère, deux copépodes, *Artemia* et *Trichocorixa verticalis*, un prédateur de la famille des *Corixidae*. Ce dernier maintient *Artemia* à de faibles densités ($<100 \cdot m^{-3}$). Cette diminution de la quantité d'*Artemia* et d'autres espèces zooplanctoniques a entraîné une diminution de la consommation d'algues de telle sorte que les taux de chlorophylle (5–44 $mg \cdot m^{-3}$) et la turbidité (profondeurs mesurées avec un disque de Secchi : 0,8 – 2,7 m) sont élevés durant toute l'année. Cela a pour effet de réduire la quantité de phosphore soluble réactif et d'zote inorganique dans le mixolimnion à des concentrations de 5 et 50 $\mu g \cdot L^{-1}$ respectivement. Le blocage des rayons lumineux par les algues dans la couche de 7 m d'épaisseur du mixolimnion et par les sulfobactéries pourpres dans le chemocline fait en sorte que les eaux du monimolimnion gardent une température presque constante (9–11°C) durant toute l'année. La prédation par *Trichocorixa verticalis* a pu avoir des effets qui se sont répercutés dans tout le système, touchant à la fois la population d'herbivores, la distribution des éléments nutritifs et la stratification thermique dans le Grand Lac Salé.

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Hypersaline lakes are excellent sites in which to study community processes because few species tolerate their saline waters, thus reducing the number of biological interactions and making it possible to observe processes that may be obscured in more complex ecosystems. Saline systems also provide opportunities to study community interactions at different levels of complexity as their species diversity changes in response to variations in salinity. The mechanisms controlling diversity in salt lakes are not, however, fully understood (Wiederholm 1980; Herbst 1988; Melack 1988; Williams 1990).

The Great Salt Lake, Utah, is a desertic terminal lake that has both temporal and spatial salinity gradients and thus provides opportunities to study community processes at different levels of species diversity. Like other terminal lakes (i.e. Jellison and Melack 1988), the Great Salt Lake's depth, volume, and salinity fluctuate widely in response to climatological cycles. Between 1963 and 1987, as the lake grew from its historic low to its historic maximum level, the salinity in its largest basin decreased from near 250 to 50 g/L.

Here we provide descriptive data on the limnology of the lake during 1985–87 when it was at its lowest recorded salinity and discuss how changes in the zooplankton at the top of the food chain may have progressively affected the phytoplankton, chemistry, and physics of the lake. Such cascading effects of top predators on successively lower levels in the food chain have been demonstrated in several aquatic systems (i.e. Paine 1980; Carpenter 1988). In addition to providing insights on trophic interactions in lakes, our study on the Great Salt Lake provides baseline information on an important system whose ecology has received comparatively little attention (Wirick 1972; Stephens and Gillespie 1976; Post 1977, 1980; Wurtsbaugh 1988).

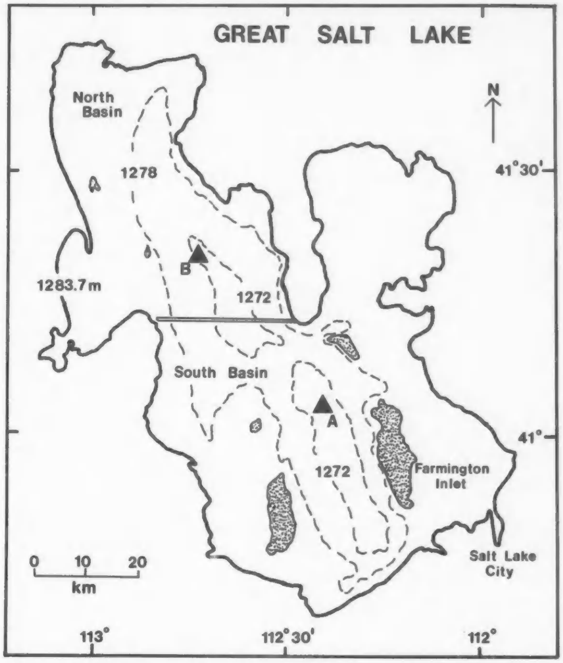

FIG. 1. Morphometry of the Great Salt Lake showing the location of sampling stations used in the study (▲). The lake is shown at its historic high level of 1283.7 m. Adapted from Stephens and Gillespie (1976) and Stephens (1990).

Study Area

The Great Salt Lake is a shallow remnant of prehistoric Lake Bonneville that covered 49 000 km^2 of the Great Basin about 15 000 yr ago (Currey 1980). During our study, the lake elevation fluctuated between 1282.8 and 1283.8 m and covered about 6000 km^2, making it the largest saline lake in the Western Hemisphere (Hammer 1986). The chemical composition of the lake is similar to that of seawater, with NaCl accounting for 85% of the total dissolved solids (Sturm 1980).

In 1959, a rock-filled railway causeway was built that separated the lake into a north and south basin. During the study the south basin of the lake, where most of our work was done, had an area of 3420 km^2, a maximum depth of 13.3 m, and a mean depth of 5.8 m. The fetch of the south basin, from the western end of the causeway to the southern end of the lake, was 65 km. The study site (Fig. 1) in the south basin was located 9 km from the nearest shore, at a location sampled by Stephens and Gillespie (1976). The collection site in the north basin was at a depth of 12 m.

The south basin of the lake receives 95% of the surface inflows and consequently has a higher elevation and a lower salinity than the north basin (Stephens and Arnow 1987), which receives water primarily through culverts linking the two systems (Fig. 1). The dense, concentrated brine in the north basin seeps back through the rock causeway and culverts (Madison 1970) and flows to the deeper portions of the south basin, maintaining it as a meromictic system (Stephens and Gillespie 1976; Sturm 1980). In 1984, a 91-m-long breach was made in the railway causeway in order to alleviate flooding around the south basin that was caused by excessively high runoff during 1982–84.

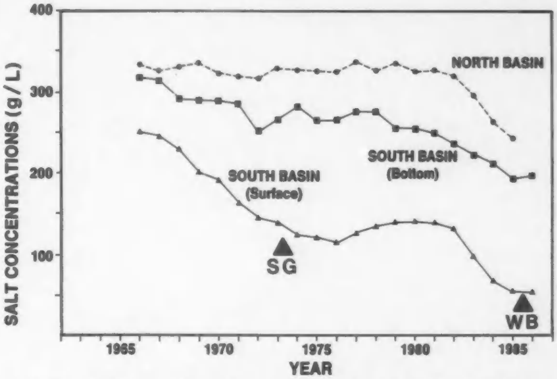

FIG. 2. Salinities of the north and south basins of the Great Salt Lake from 1966 to 1986. Periods of intensive study on the plankton are noted by "SG" (Stephens and Gillespie 1976) and "WB" (present study). Data collected by the Utah Geological and Mineral Survey.

Relatively few organisms tolerate the saline waters in the lake and consequently the community is depauperate. Rushforth and Felix (1982) reported that there were 20 species of algae and 10 species of protozoa in the south basin when salinities were 115 g/L. Two species of brine flies (*Ephydra* spp.) were abundant in the littoral areas, and the corixid *Trichocorixa verticalis* was found in bays, marinas, and along the margins of islands. Prior to our study the only pelagic macrozooplankton reported was the brine shrimp *Artemia salina* (Rushforth and Felix 1982). Bowen et al. (1985) have recently reclassified brine shrimp from the Great Salt Lake into the *A. franciscana* superspecies.

Methods

We made a year-long series of collections in the south basin of the Great Salt Lake during 1985–86. In June 1986 we made one additional collection in the north basin, and in April 1987 we collected detailed vertical profiles on a variety of parameters in the south basin.

Density and salinity data were provided by the Utah Geological and Mineral Survery. Water for these measurements was collected with a pump and transported to the laboratory where density was measured with ASTM hydrometers. Concentrations of the major ions were also measured (Sturm 1980) and we calculated the following regression between density and salinity (sodium, magnesium, potassium, calcium, chloride, and sulfate):

$$\text{Salinity (g/L)} = 1430.6\ (\text{density}) - 1430.8 \qquad (R^2 = 0.997,\ n = 37).$$

We measured temperature profiles with a Yellow Springs Instrument thermistor (precision = 0.1°C) and photosynthetically active radiation (PAR) with a model 188B LiCor quantum radiometer equipped with a 4-Pi sensor. We calculated extinction coefficients as the slope of the regressions relating depth and the natural logarithm of percent light transmission. We used a 20-cm Secchi disk with two white and two black quadrants to measure transparency.

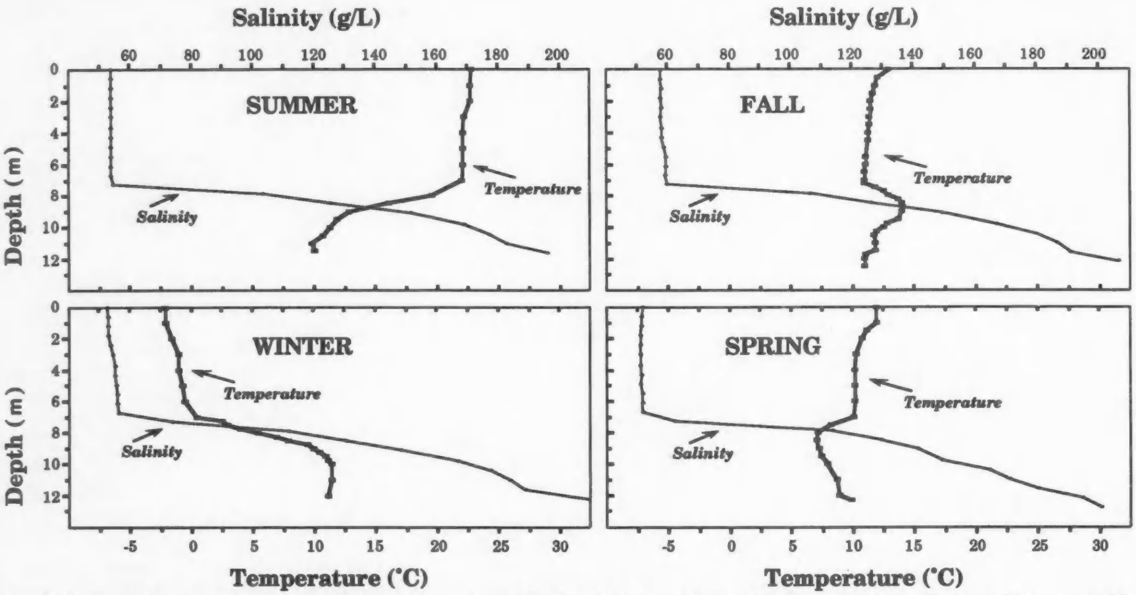

FIG. 3. Seasonal changes in the vertical profiles of temperature and salinity in the south basin of the Great Salt Lake. Summer, 21 August 1985; fall, 29 October 1985; winter, 21 January 1986; spring, 14 April 1986.

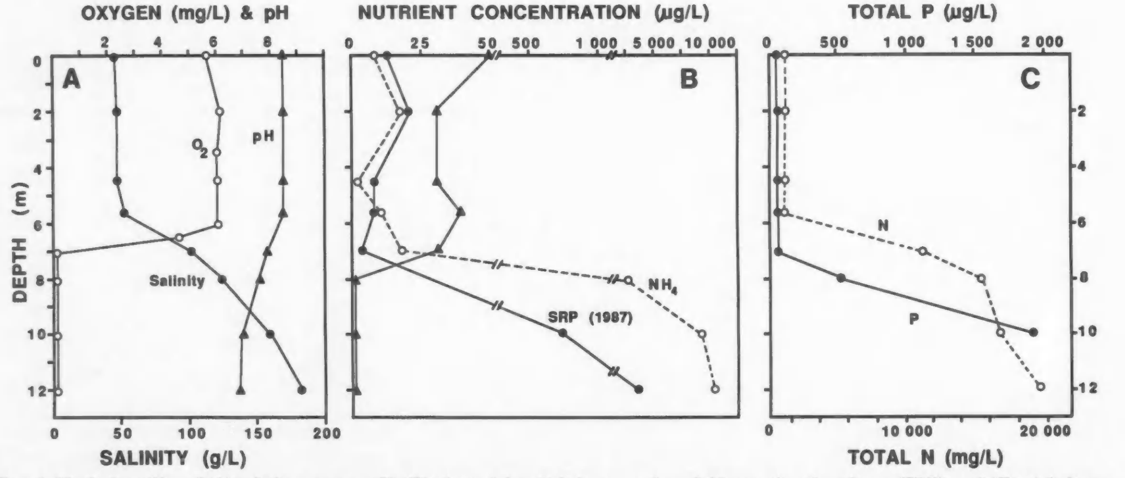

FIG. 4. Vertical profiles of (A) salinity, oxygen, pH, (B) nitrate (plus nitrite), ammonia, soluble reactive phosphorus (SRP), and (C) total nitrogen and phosphorus in the Great Salt Lake on 25 April 1987. Concentrations of phosphorus below 8 m are only approximate (see Methods).

We collected water for chemical analyses with a 10-L Kemmerer bottle. Oxygen was analyzed with the azide modification of the Winkler method (American Public Health Association (APHA) 1980). Titrations were performed in the field with 0.25 N thiosulfate and a microburette. The pH was measured potentiometrically in the laboratory within 6 h of sample collection.

We filtered samples for dissolved nutrient analyses through both acid-washed glass fiber (Whatman GF/C) and 0.45-µm membrane filters and then froze them. Because of the high concentration of nutrients in the monimolimnion, these samples were diluted 1:4 or 1:10 with deionized water prior to analysis. We analyzed soluble reactive phosphorus (SRP) with the molybdate blue method (Wetzel and Likens 1979). Total phosphorus was measured after persulfate digestion (APHA 1980), ammonia by the indophenol method, nitrate (plus nitrite) by an automated cadmium reduction technique, and total nitrogen by Kjeldahl analysis (APHA 1980).

For all analyses except phosphorus, the recovery of internal standards was greater than 95%. However, the recovery of SRP from monimolimnetic water was only 10–20%, indicating strong interference. Reported values were corrected for the percent recovery of internal standards. Percent recovery of total phosphorus in the monimolimnion was not measured, however. The concentrations of phosphorus from this stratum are therefore only approximate.

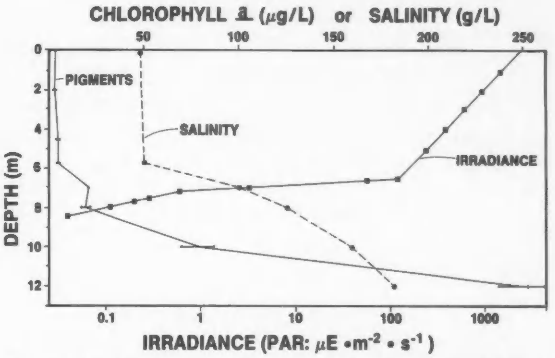

FIG. 5. Changes in light intensity and chlorophyll *a* in relation to chemical stratification in the Great Salt Lake (25 April 1987). Error bars for chlorophyll show the range of duplicate determinations at each depth.

Samples for chlorophyll and phaeophytin analyses were filtered on 0.45-μm membrane filters, frozen, and subsequently extracted in boiling 100% methanol and analyzed fluorometrically (Holm-Hansen and Riemann 1978) with a Turner model 111 fluorometer calibrated with standard chlorophyll *a* (Sigma Chemical Co.). The absorbance spectra of the pigments in seston were measured on glass fiber filtered samples that were extracted into 100% buffered acetone for 24 h at room temperature. The spectra were measured on a Bausch and Lomb model 710 spectrophotometer with a slit width of 2 nm.

During 1985–86 we made duplicate vertical zooplankton hauls from the bottom to the surface with a 30-cm-diameter Wisconsin net usually fitted with 80-μm Nitex netting. Zooplankton were preserved with Lugol's solution (Lind 1979). We counted the entire sample for brine shrimp and Corixidae and subsampled other taxa with a Hensen–Stempel pipette to give counts of >50 organisms. In April 1987 we measured the vertical distribution of *Artemia* by making duplicate collections at several depths with a 50-L Schindler plankton trap fitted with 80-μm Nitex netting.

Results

Salt concentrations in the different basins and strata of the Great Salt Lake have fluctuated widely during the past 20 yr. Salinity in the surface waters of the south basin decreased from 250 g/L in 1963 to 50 g/L in 1985–86 (Fig. 2). Salt concentrations in the bottom of monimolimnion also declined from over 300 g/L in 1966 to near 200 g/L during our study. In the north basin, salinities were near saturation (325 g/L) until after 1982, when the unusually high precipitation in the watershed diluted these waters to below 250 g/L.

Strong salinity gradients in the south basin chemically stratified the water column (Fig. 3). Salinity differences of 1–3 g/L occurred within the 6.5- to 7.5-m-thick mixolimnion during the fall and winter. Below the mixolimnion, salinity increased rapidly, reaching nearly 200 g/L at 11–12 m.

Temperatures within the mixolimnion were generally uniform, except for 1–2°C differentials caused by diurnal surface heating or maintained by the slight chemical stratification. Subsequent to this study, however, we have observed thermal gradients of up to 5°C in the mixolimnion during the spring (W. Wurtsbaugh, unpubl. data). Seasonally, temperatures in the mixolimnion varied from −2°C in January to 23°C in August (Fig. 3, 7). The lake does not freeze, but snow sometimes accumulates and compacts on portions of the supercooled surface. Seasonal thermal changes in the chemocline were slower than in the mixolimnion, resulting in bulges in the vertical temperature profiles during the fall and spring, as heat was lost to, or gained slowly from, the upper layer (Fig. 3). In the monimolimnion, temperature varied only between 9 and 11°C over the annual cycle.

Chemical profiles measured in April 1987 showed the strong effects of meromixis. Below the mixolimnion, the water rapidly became anoxic, pH dropped from 8.4 to 6.9 (Fig. 4A), and the odor of H_2S was noted. Ammonium concentrations in the mixolimnion varied from 2 to 19 μg/L but increased to 10 000 μg/L in the monimolimnion (Fig. 4B). Nitrate (plus nitrite) was near our limit of detection (40 μg/L) in the mixolimnion but was undetectable in the chemocline and monimolimnion. SRP in the surface layer was 9–20 μg/L, decreased to 4 μg/L in the chemocline, where there was a dense population of purple-sulfur bacteria (see below), and then increased to over 3000 μg/L in the monimolimnion (Fig. 4b). Total nitrogen and phosphorus concentrations in the mixolimnion were near 1400 and 80 μg/L, respectively. In the monimolimnion, concentration of total nitrogen reached 19 400 μg/L (Fig. 4C).

Light penetration and pigment distribution were strongly affected by the vertical stratification (Fig. 5). Characteristic results are shown for 25 April 1987, when the Secchi depth was 2.0 m. In the mixolimnion, the extinction coefficient (η) was 0.44/m, and the light intensity decreased to 6% of the surface value at the top of the chemocline (6.5 m). The concentration of chlorophyll *a* in the mixolimnion was 3–4 mg/m^3, and the spectral signature (not shown) was characteristic of chlorophyll *a* and phaeophytin. In the upper portion of the chemocline (6.5–7.2 m) light extinction was rapid ($\eta = 9.95$/m), and light dropped to <1 μE·m^{-2}·s^{-1} at the bottom of this layer. This stratum was colored bright pink, and purple-sulfur bacteria (family Chromatiaceae) were abundant. The spectral signature from this layer had a major peak at 770 nm (Fig. 6), indicating that bacteriochlorophyll *a* was dominant (Goedheer 1966).

Large amounts of chlorophyll accumulated in the deep monimolimnion. Below the layer of purple-sulfur bacteria the water was colored a dark green–brown. The vertical extinction coefficient in this deep layer was 2.14/m (Fig. 5). Chlorophyll *a* and phaeophytin concentrations of the seston here reached high levels of 230 and 270 mg/m^3, respectively. These bottom waters contained large amounts of both dissolved pigments and intact algal cells. The spectral signature of seston from the monimolimnion had a peak of 665 nm (Fig. 6), a major absorption peak for chlorophyll *a*. The large amount of chlorophyll and the abundance of intact algal cells in the monimolimnion suggest that organisms fail to sediment out in the dense water (specific gravity of 1.09 – 1.14) and that the brine, low light, and anoxic conditions may prevent the degradation of chlorophyll *a* to phaeophytin (Daley and Brown 1973).

During 1985–86, seasonal variations in light transmission (Fig. 7) and chlorophyll (Fig. 8A) were relatively small in comparison with the marked vertical gradients of these parameters. Secchi depths varied from a minimum of 0.8 m in the fall and winter to a maximum of 2.7 m in June, with a corresponding range of extinction coefficients from 0.80 to 0.39/m. Chlorophyll *a* in the mixolimnion was lowest in spring (5–10 mg/m^3), peaked at 44 mg/m^3 in August 1985, and remained between 15 and 25 mg/m^3 during the fall and winter (Fig. 8A). Additional

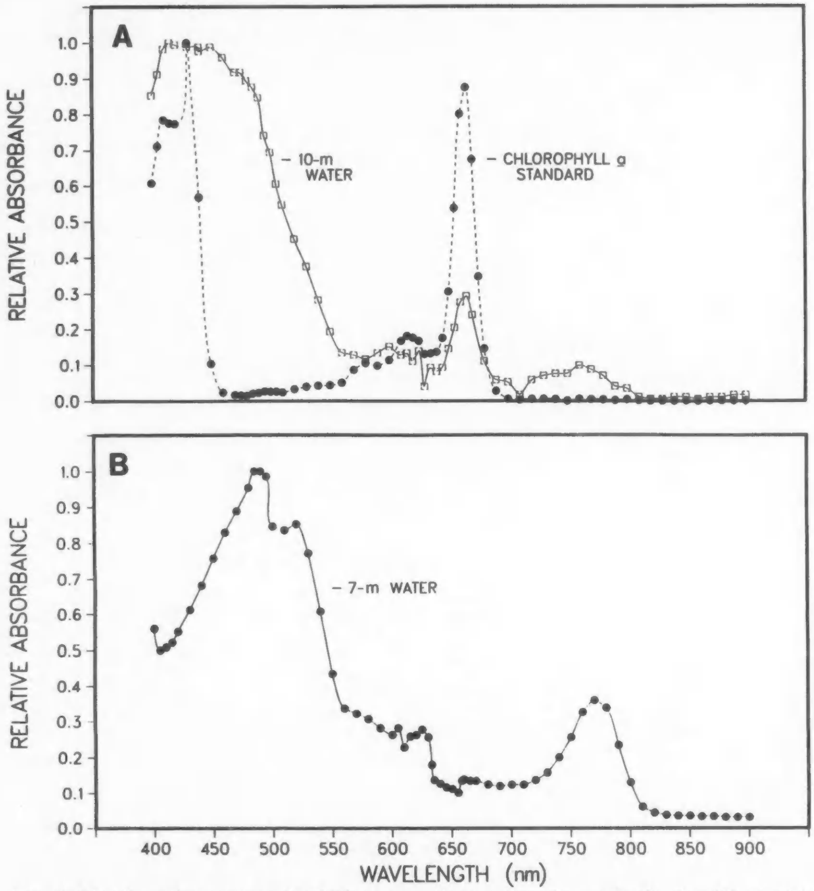

FIG. 6. (A) Absorption spectrum in 100% acetone of seston from the monimolimnion (10 m) of the Great Salt Lake. The spectrum of chlorophyll *a* (Sigma Chemical Co.) in 100% acetone is also shown for comparison. (B) Absorption spectrum of the seston containing purple-sulfur bacteria from the chemocline (7 m) of the lake. The samples were collected 25 April 1987.

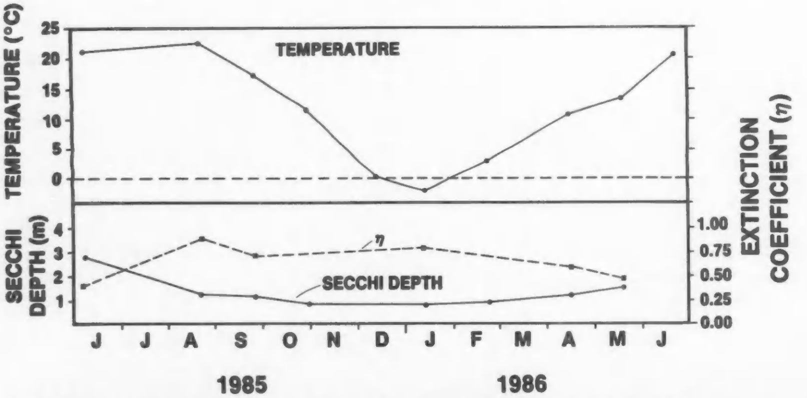

FIG. 7. Seasonal variations in the temperature (1 m depth), Secchi depth, and extinction coefficient of the mixolimnion of the Great Salt Lake (south basin).

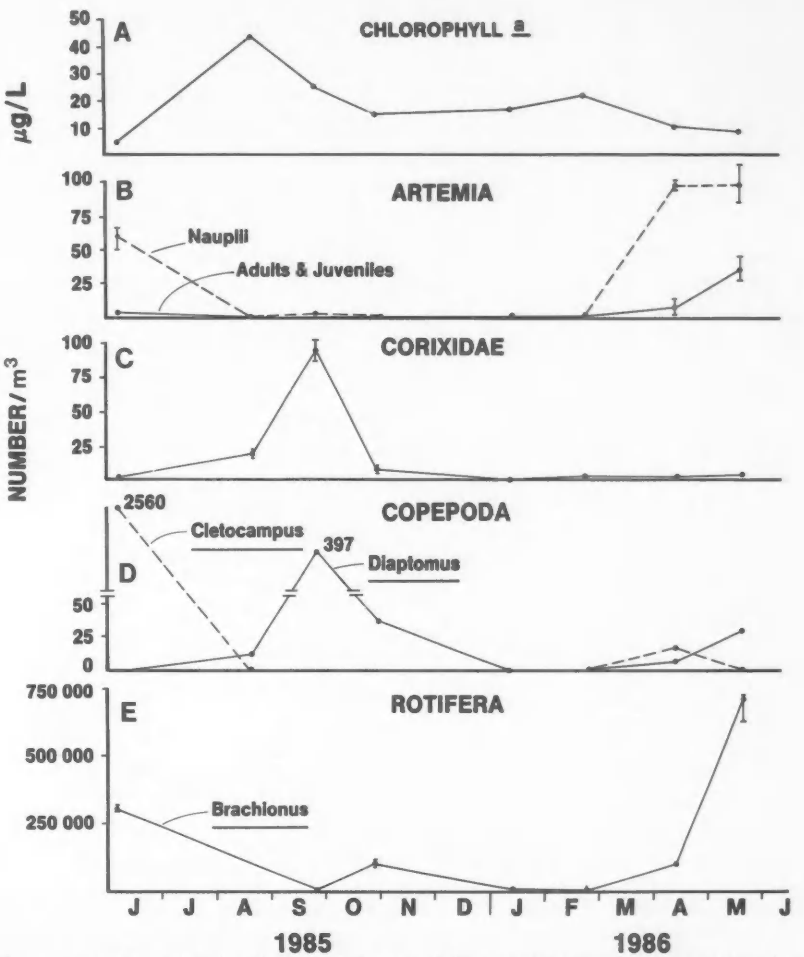

FIG. 8. Seasonal variations in (A) chlorophyll *a*, and (B–E) the zooplankton populations in the mixolimnion of the Great Salt Lake (south basin). Chlorophyll concentrations shown are the means of four to six samples collected throughout the mixolimnion on each date. Densities of *Brachionus* sp. are not graphed for the August collection because on that date we used a coarse-mesh zooplankton net (153 μm) which would have missed small plankton. Error bars show ranges for duplicate collections at a single station and consequently do not indicate variance due to large-scale spatial heterogeneity.

chlorophyll readings we have taken in other regions of the south basin of the Great Salt Lake have ranged as high as 224 mg/m^3 in Farmington Inlet, an area affected by urban discharges (W. Wurtsbaugh, unpubl. data). Although we did not count or identify the phytoplankton present in the lake, occasional microscopic observations indicated that cyanobacteria (*Nodularia* sp.), diatoms, and other plankton were present.

In contrast with the relative stability of chlorophyll *a* levels throughout the year, seasonal variations in *Artemia* were marked. In the south basin the density of *Artemia* was very low throughout most of the year, but peaked in the spring (May–June). At maximum abundance, however, nauplii and postnauplii in this basin reached concentrations of only 99 and 37/m^3, respectively (Fig. 8B). The ovigerous *Artemia* were collected in May 1986 had white eggs that were larger than overwintering cysts, indicating that the shrimp were reproducing ovoviviparously.

Abundances of the other zooplankton were also highly seasonal. The predatory corixid *T. verticalis* was absent or rare during the winter and spring, but reached a peak abundance of 96/m^3 (670/m^2) in late summer (Fig. 8C). The average length of corixids was 3.0 mm (range 1.4–4.5 mm). Two copepods were present in the lake, but they were not usually abundant (Fig. 8D). The harpactocoid *Cletocampus albuquerquensis* had a moderate density of 2560/m^3 in June 1985, but subsequently was found on only one other date. The calanoid *Diaptomus connexus* occurred more consistently during the year, but it had a maximum density of only 397/m^3 in September. The most abundant zooplankter was the small (~0.2 mm) rotifer *Brachionus* sp (probably *B. plicatilis*), which reached densities of

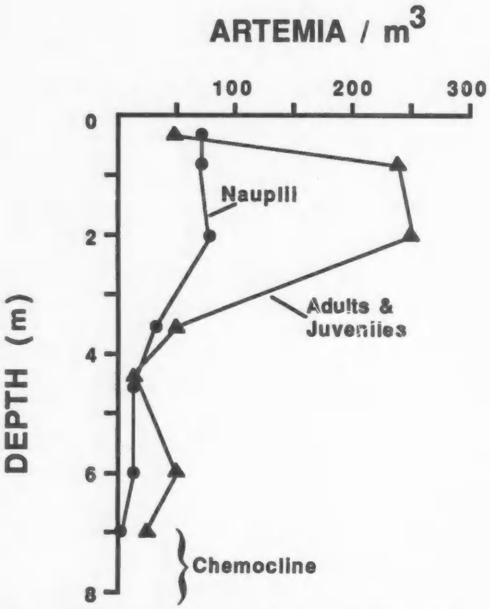

FIG. 9. Vertical distribution of *Artemia franciscana* in the Great Salt Lake at 1400 on 25 April 1987. The densities shown are means of two replicate Schindler trap catches at each depth.

at least 260 000 and 745 000/m^3 in the spring of 1985 and 1986, respectively (Fig. 8E).

The vertical profile of *Artemia* demonstrated that they were concentrated in the upper portion of the mixolimnion (Fig. 9). Nauplii were most concentrated between the surface and 2 m, while subadults and adults were most abundant between 1 and 2 m.

Discussion

Meromixis and Productivity

Meromixis in the south basin of the lake provides only partial separation between its layers because the large fetch (65 km; Fig. 1) allows wave action and turbulence to continually erode water of the chemocline and the monimolimnion into the mixolimnion (A. Lin, Utah Division of Water Resources, Salt Lake City, UT, unpubl. data). The slightly greater salinities we observed in the lower portion of the mixolimnion on some dates (Fig. 3) may have been transient occurrences caused by entrainment of chemocline water into the mixolimnion during fall and winter storms. Alternatively, these salinity discontinuities could have been caused by freshwater inflows mixing into the surface layers of the mixolimnion.

The residence time of water in the monimolimnion can be approximated using its volume and the flow rate of brine through the causeway. Waddell and Bolke (1973) found this flow to be between 1.1 and 1.7 km^3/yr, and the volume of the monimolimnion and chemocline layers (depth >7 m) is 4.3 km^3 (G. Pyper, U.S. Geological Survey, Salt Lake City, UT 84104, USA, unpubl. data). These flows and volume yield turnover times for the monimolimnion ranging from 2.5 to 3.9 yr. Although the flow rates would vary considerably with changes in head and density differences between the two basins, it is clear that the monimolimnetic water of the Great Salt Lake could be entrained rapidly into the mixolimnion.

The eutrophic condition of the lake may be due to the entrainment of the nutrient-laden water from the monimolimnion into the photic zone. Although chlorophyll concentrations in the lake are relatively low in relation to other salt lakes (Hammer 1986), its mean chlorophyll concentration of 18 mg/m^3 (Fig. 7A) indicates that it is eutrophic (Wetzel 1983). If sedimenting nutrients were trapped permanently in the monimolimnion, productivity might be reduced considerably (see Jellison and Melack 1988). Additionally, the monimolimnion underlies only 38% of the surface area of the south basin of the Great Salt Lake, so that much of the sedimenting material never falls into this layer and may be recycled at even higher rates than calculated for the turnover time of the monimolimnion.

Cascading Effects of the New Plankton Community

Decreasing salinity in the Great Salt Lake has permitted several species of zooplankton to invade, and this has apparently affected the phytoplankton, nutrients, and thermal stratification of the system. When the lake's salinity was greater than 125 g/L, the only metazoan organism reported in the pelagic region was *A. salina* (Post 1977; Rushforth and Felix 1982), but during our study, when the salinity was 50 g/L, there were five species. The previous absence of *T. verticalis*, *B. plicatilis*, and *D. connexus* was consistent with their maximum salinity tolerances of 90, 97, and 107 g/L (Walker 1981; Tones and Hammer 1975; Hammer 1986). The salinity tolerance of *C. albuquerquensis* (>300 g/L) is much higher (Hammer 1986), so it is doubtful that chemical factors limited it previously. Competition with large populations of *Artemia* may have contributed to the absence of this species when the lake was more saline (see below).

In addition to the appearance of new taxa, one of the more striking changes in the zooplankton assemblage was the large decrease in the abundance of *Artemia*. Previously, populations of postnaupliar *Artemia* reached 5000 – 18 000 organisms/m^3 in May and June and then collapsed when the phytoplankton populations were grazed down (Wirick 1972; Stephens and Gillespie 1976; Gillespie and Stephens 1977). The maximum density of postnaupliar *Artemia* we found in the south basin was only 37/m^3 (Fig. 7). Had we sampled more intensively or for a longer period, we undoubtedly would have encountered higher densities, but it is clear that populations of *Artemia* have declined markedly from those reported earlier. The demise of the brine shrimp in the south basin stopped the commercial harvest of cysts, once reaching 77 t, from this basin (Stephens 1990).

It is unlikely that this brine shrimp decline was a direct result of changing salinity on their survival. Physiologically, brine shrimp thrive at salinities below that of seawater (35 g/L) (Persoone and Sorgeloos 1980), and maximum survival rates occur near the salinity we encountered in the south basin (50 g/L) (Bowen et al. 1985). It also seems unlikely that salinity-induced changes in the reproductive mode of *Artemia* (Dana and Lenz 1986) contributed to the decline. The presence of ovoviviparous females in our spring collections suggests that the population of *Artemia* had not then switched to oviparous reproduction, as has been indicated for a sibling species (Dana and Lenz 1986). Unfortunately, no oviparous females were collected during the summer due to their very low density, so it was not possible to determine how long the ovoviviparous mode of reproduction was continued.

Stephens (1990) suggested that the decline in *Artemia* abundance was due to the lower density of the water that caused the overwintering cysts to sink to the bottom where they could not be hydrated by dilute spring runoff. D'Agostino (1965, cited by Collins 1977), however, indicated that salinities below 99 g/L do not completely repress hatching of *Artemia* cysts from the Great Salt Lake, so it is possible that the submerged cysts could hatch.

While the sinking of the cysts may nevertheless contribute to the decline of *Artemia*, it cannot explain the greatly reduced summer populations. When the salinity of the Great Salt Lake was near 130 g/L, population growth rates of *Artemia* reached 10%/d (calculated from 1971 data of Gillespie and Stephens 1977). In the spring of 1985 we found nauplii densities of 60/m^3. At the growth rates found by Gillespie and Stephens (1977), populations of *Artemia* should have reached 20 000/m^3 within 60 d. In actuality, the population declined to less than 1/m^3 over this time period. Other factors therefore must be affecting the population.

The loss of *Artemia* in the summer may have been due to predation by *T. verticalis*. Limited experimental work by Hayes (1971) indicated that *T. verticalis* can consume five nauplii or one adult *Artemia* per day, and Reynolds (1975) indicated that it is a top predator in small alkaline lakes of Canada. The vertical distribution of the corixid also overlaps broadly with *Artemia* (Fig. 9), as Hayes (1971) found that the insect dove to at least 3.6 m in an estuary of the Great Salt Lake. Furthermore, Hayes (1971) and Carpelan (1957) have reported inverse correlations between densities of *Artemia* and *Trichocorixa* along salinity gradients in the Great Salt Lake and Alviso Salt Ponds, respectively. During our study, *T. verticalis* reached densities of 20 and 96/m^3 in August and September, much higher than densities of *Artemia*. The predation rate, densities, and distribution of the corixids suggest that they could have controlled *Artemia* populations. In addition, the increasing abundance of *T. verticalis* in the spring and summer was associated with the decline in *Artemia*, also supporting the hypothesis that the predator was controlling the brine shrimp (Fig. 7). Invertebrate predators in other aquatic systems frequently control prey populations and affect community structure (i.e. O'Brien 1979; Paine 1980; Peckarsky and Dodson 1980).

The decline of *Artemia* had a large impact on the algae, physics, and chemistry of the Great Salt Lake. Before *T. verticalis* invaded the pelagic zone, the dense populations of *Artemia* (7000 – 18 000/m^3), filtering at rates up to 350 $mL \cdot individual^{-1} \cdot d^{-1}$ (Reeve 1963), contributed to 50-fold decreases in algal abundance following the spring bloom. When *Artemia* were abundant, Secchi depths changed from <1 m during the spring bloom to 5–8 m after late-instar *Artemia* increased in May (Stephens and Gillespie 1976; Gillespie and Stephens 1977; Montague 1982). In contrast, during 1985–86, the small populations of *Artemia* (<100/m^3) and other zooplankton in the south basin were unable to clear the water column, and chlorophyll levels remained high (5–44 mg/m^3) and Secchi depths low (<2.2 m) throughout the year. The low densities of recently colonized copepods, coupled with the low grazing rates of the copepods (1–2 $mL \cdot invididual^{-1} \cdot d^{-1}$) and rotifers (0.01–0.2 $mL \cdot individual^{-1} \cdot d^{-1}$) (Allan 1976), apparently prevented the new zooplankton assemblage from affecting the algae to the same degree as did the large population of *Artemia*. The capacity of *Artemia* to decrease algal abundance and increase clarity was manifested in the north basin of the Great Salt Lake. On our single visit to this basin (Station B; Fig. 1) on 17 June 1986 we found a large population of postnaupliar *Artemia* (6750/m^3), a Secchi depth of 9.1 m, and an epilimnetic chlorophyll *a* concentration of only 0.2 mg/m^3. *Trichocorixa verticalis* were absent. In contrast, when salinities in the north basin were near saturation and brine shrimp densities were very low (1/m^3), the Secchi depth was less than 0.5 m (F. Post, Utah State University, Logan, UT 84322-5500, USA, pers. comm.). The ability of *Artemia* to greatly reduce phytoplankton populations has been noted previously for the Great Salt Lake (Montague 1982) and elsewhere (Lenz 1982; Jellison and Melack 1988).

This food chain effect on water transparency also influenced the thermal structure of the south basin of the Great Salt Lake. When *Artemia* were abundant and Secchi depths were 5–8 m, light penetrated into the monimolimnion and heated it from less than 10°C in April to 24°C by August (Stephens and Gillespie 1976). With the low Secchi depths and high extinction coefficients found in our study (Fig. 7), a maximum of 0.1% of surface radiation penetrated to the top of the monimolimnion, and temperatures in the deep water remained near 10°C throughout the year (Fig. 3).

The changes in algal populations may have also affected the nutrient chemistry of the lake. When *Artemia* were abundant and phytoplankton populations low, SRP and NH_3 in the mixolimnion were near 600 and 100–300 μg/L, respectively (Stephens and Gillespie 1976). In contrast, we found only 10–20 μg SRP/L and 10 μg NH_4/L in the mixolimnion during our April 1987 analyses (Fig. 4). Additional analyses of mixolimnion water collected 16 April 1988 yielded SRP concentrations of 20 ± 2 μg/L (SD) similar to those found in 1987 (W. Wurtsbaugh, unpubl. data). The high algal populations that occurred in the absence of *Artemia* grazing may have reduced concentrations of dissolved nutrients to low levels.

The nutrient chemistry of the lake may also have been altered by changes in algal community composition. When the lake's salinity was near 200 g/L, the phytoplankton community was nearly a monoculture of *Dunaliella viridis*, and nitrogen-fixing cyanobacteria were absent or rare in the pelagic region of the lake (Rushforth and Felix 1982). Samples we collected during our study contained nitrogen-fixing *Nodularia* sp., and acetylene reduction rates to 200 $nmol \cdot L^{-1} \cdot h^{-1}$ have been measured in Great Salt Lake water (Wurtsbaugh 1988). Despite this high rate of fixation, nitrogen continues to be a limiting nutrient in the system (cf. Stephens and Gillespie 1976; Wurtsbaugh 1988). Nitrogen fixation by the cyanobacteria must increase the nitrogen budget of the lake, and this may prolong the bloom of algae into the summer months (Fig. 8A). When the lake was saltier and nitrogen-fixing cyanobacteria absent, nitrogen deficiency may have contributed to the summer decline in phytoplankton (Stephens and Gillespie 1976).

Another apparent change in the Great Salt Lake that occurred with decreasing salinity was the growth of a dense population of purple-sulfur bacteria in the chemocline. The moderate to intense pink color of this layer was very distinctive during our study. Since the construction of the rock-filled causeway in 1959, the lake has been meromictic (Stephens and Gillespie 1976) and presumably has provided conditions (H_2S, light) at the chemocline for purple-sulfur bacteria (Takahashi and Ichimura 1970; Northcote and Hall 1983). Nevertheless, despite efforts to locate them, these bacteria were not found during the intensive investigation of Stephens and Gillespie (1976) and D.

Stephens (U.S. Geological Survey, Salt Lake City, UT 84105, USA, pers. comm.). A less intensely colored thin layer (~4–5 cm) of these bacteria was first noted in 1978–79 (F. Post, Utah State University, Logan, UT 84322-5500, USA, unpubl. data), but during our recent observations this layer was at least 100 cm thick.

Our study demonstrates that the decreasing salinity of the Great Salt Lake greatly modified the zooplankton and phytoplankton communities. Changes in predation and/or grazing intensity of the zooplankton, in turn, may have caused a cascading effect on the phytoplankton, chemistry, and even the physics of the lake. A preliminary microcosm experiment done in our laboratory has demonstrated that the addition of *T. verticalis* to the community can cause many of the types of changes we observed in the lake between Stephens and Gillespie's (1976) earlier study and our own (W. Wurtsbaugh, unpubl. data). This adds additional support to the hypothesis that this invertebrate is structuring the community in the lake. Nevertheless, additional descriptive studies and field experiments will be necessary to determine if this predator is dominating the biotic, chemical, and physical interactions of this interesting salt lake.

Postcript

Since our study, precipitation in the Great Salt Lake basin has decreased, the lake level has dropped, salinites have increased to over 100 g/L, and *Artemia* have returned to high densities to the south basin (D. Stephens, pers. comm.).

Acknowledgments

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Zooplankton Species Associations in Quebec Lakes: Variation with Abiotic Factors, Including Natural and Anthropogenic Acidification[1]

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Abundances and biomass of 38 zooplankton species and accompanying abiotic data from 54 Quebec lakes were subjected to cluster and correlation analysis to determine (1) characteristic zooplankton associations of cooccurring species, (2) relative importance of abiotic variables in lake typology, and (3) relationships between the integrated environmental factors derived from lake morphometry, water quality, and acidification level, and the structure of zooplankton communities. The eight groups of species identified in the cluster analysis may be considered separate "species associations" characterized by distinct patterns of distribution in Quebec lakes. Differences in mean pH and sulphate concentrations can be detected between groups of lakes representing the different species associations. Factor analysis produced seven factor scores which explain 82% of the total variance of the morphological, physical, and chemical variables. The distribution pattern of acidity or alkalinity represents the major feature in water chemistry variation, but lake morphology also account for the observed environmental variability. Each factor represents an integrated environmental property correlated with a set of colinear abiotic variables. These factors are correlated with zooplankton species abundances and biomass. The community structure, whether expressed in size classes or in trophic groups, tends to vary among sets of lakes of different pH.

L'abondance et la biomasse du zooplancton ainsi que les caractéristiques abiotiques de 54 lacs du Québec ont fait l'objet d'analyses factorielles et d'analyses de corrélation visant à déterminer 1) les associations d'espèces représentatives de la variabilité du zooplancton, 2) l'importance relative des variables abiotiques pour la typologie des lacs et 3) les relations entre les principaux facteurs environnementaux reliés à la morphométrie des lacs, à la physico-chimie des eaux et aux niveaux d'acidification, et la structure des communautés zooplanctoniques. Les huit associations d'espèces déterminées par groupement à liens complets peuvent être considérées comme des associations distinctes par leur patron de répartition dans les lacs du Québec. Des différences entre les valeurs moyennes de pH et de sulfates peuvent être détectées entre les groupes de lacs représentatifs des différentes associations d'espèces. L'analyse factorielle a déterminé sept facteurs environnementaux qui expliquent 82 % de la variance totale de la morphométrie et de la physico-chimie des lacs. Le patron de distribution de l'acidité ou inversement de l'alcalinité, représente la majeure partie de la variabilité mais la morphométrie des lacs influence aussi la variabilité observée dans les conditions abiotiques. Chaque facteur représente une caractéristique environnementale composite corrélée à un ensemble de variables abiotiques colinéaires. Ces facteurs ont été corrélés avec l'abondance et la biomasse des zooplanctontes. La structure de la communauté, exprimée soit en classes de taille ou en groupes trophiques est variable selon les groupes de lacs de pH différent.

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The spatial analysis of freshwater zooplankton with reference to acidification has been investigated mainly with respect to crustacean plankton community structure and lake typology (Sprules 1975; Yan and Strus 1980; Keller and Pitblado 1984; Pinel-Alloul et al. 1987). Kelso et al. (1986) published a comprehensive study of the relationships between the coarse composition and diversity of the aquatic biota and the physical and chemical conditions prevailing in eastern Canada lakes but failed to define general trends in occurrence and abundance of zooplankton species in relation to pH. Similar studies were carried out at a regional level by Pinel-Alloul and Méthot (1985) and Pinel-Alloul et al. (1987) in Quebec lakes. In acidified regions of Ontario, much research (Sprules 1975; Roff and Kwiatkowski 1977; Yan and Strus 1980; Confer et al. 1983; Malley and Chang 1986) has been conducted to determine species associations in relation to lake pH. According to Sprules (1977), patterns of variability in a large group of species provide more information about the habitat than does variation in a single species. It was thus decided to use species associations or communities as indicators of lake acidity and typology.

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Although the part of Quebec lying on the Canadian Shield has often been recognized as an area of high sensitivity to acidification (Harvey et al. 1981; Lachance et al. 1984), little emphasis has been given to the acidification of Quebec surface waters with respect to its relationship to aquatic biota, especially in the case of planktonic organisms. Our major objectives in this study were to (1) describe the structure of zooplankton communities in Quebec lakes and their characteristic associations of cooccurring species, (2) determine the relative importance of the abiotic variables (morphometry, water quality, acidification indices) in lake typology, and (3) document the relationships between the critical environmental variables derived from lake morphometry, water quality, and acidification level and the organization of the zooplankton community. More specifically, the definition of the effects of acidification on zooplankton, a key component of the food web, may aid in the interpretation of field monitoring data.

Materials and Methods

Study Area

A number of morphometric, physical, chemical, and biotic variables were measured in 54 lakes of first, second, and third hydrologic order throughout Quebec (Langlois et al. 1983; Pinel-Alloul and Méthot 1985). Means and ranges are presented in Table 1. The lakes sampled are located on the Canadian Shield, north of the St. Lawrence River and south of the 52°N latitude (Fig. 1), a region considered highly sensitive to acidification (Bobée and Lachance 1984; Lachance et al. 1984; Dupont and Grimard 1986), mainly because of the composition of its bedrock (gneiss–granitic) and the average pH of rainfall in Quebec (pH = 4.2 – 5.0). Most of the chosen lakes were summer stratified, easily accessible, and not affected by any human or agricultural activity in the immediate watershed. Based on principal component and hierarchical cluster analyses of the 20 physical and chemical variables (Table 1), Pinel-Alloul and Méthot (1985) have already observed a southwest to northeast longitudinal gradient in the hydrogen ion concentration, indicating that lakes of the northeastern regions (regions 05 – 07) are generally more acidic than lakes situated in the Maniwaki region (region 04) (Fig. 1). Sulphate concentrations follow an inverse gradient and it appears that sulphate levels and anthropogenic acidification are higher in southwestern Quebec lakes (Lachance et al. 1984; Pinel-Alloul et al. 1987; Dupont 1988). A recent integrated study of spatial variation in physicochemical quality in our lakes (Department of Fisheries and Oceans 1987) showed that 72% of the lakes

TABLE 1. Mean and range of selected morphometric, physical, and chemical characteristics of the 54 study lakes in Quebec.

Characteristic	Mean	Minimum	Maximum
Morphometric			
Latitude	—	46°05′	51°37′
Longitude	—	63°32′	77°08′
Altitude (m)	362.1	76	655
Maximum depth (m)	21.1	4.0	83.0
Mean depth (m)	5.0	1.17	16.17
Relative depth (%)	1.4	0.2	4.1
Lake maximal length (km)	3.4	1.6	7.0
Lake maximum width (km)	1.2	0.4	2.5
Lake area (ha)	208.4	36.0	721.0
Watershed area (ha)	3855.5	261.0	29843.0
Lake volume (10^4/m^3)	3741.4	180.0	23143.0
Lake order	1.5	1	3
Lake volume development	0.8	0.3	2.1
Morphoedaphic index	7.5	0.6	49.2
Physical and Chemical			
Secchi disk (m)	3.7	1.0	8.0
Color (U.H.)	35.6	5.0	80.0
Conductivity (μS·cm^{-1}))	22.3	6.0	130.0
Hydrogen (H^+) (μeq·L^{-1})	0.9	0.01	5.58
pH	6.0	5.2	8.3
Alkalinity (μeq·L^{-1})	107.5	1.0	585.0
Cl (μeq·L^{-1})	11.8	3.0	25.0
SO_4 (μeq·.L^{-1})	76.4	20.8	229.1
Ca (μeq·L^{-1})	125.6	16.0	678.6
Mg (μeq·L^{-1})	43.4	6.3	225.3
P (μeq·L^{-1})	6.6	1.3	14.6
Na (μeq·L^{-1})	24.3	11.3	46.1
Total Al (μg·L^{-1})	104.5	14.0	228.0
Mn (μg·L^{-1})	11.8	1.0	40.0
Fe (μg·L^{-1})	98.0	14.0	356.0
Zn (μeq·L^{-1})	6.5	2.0	17.0
Dissolved organic carbon (mg·L^{-1})	5.9	2.0	11.0
Total organic carbon (mg·L^{-1})	6.1	3.0	11.0
Nitrate (μeq·L^{-1})	0.19	0.08	0.97
Alkalinity/sulphate ratio	1.26	0.01	8.70

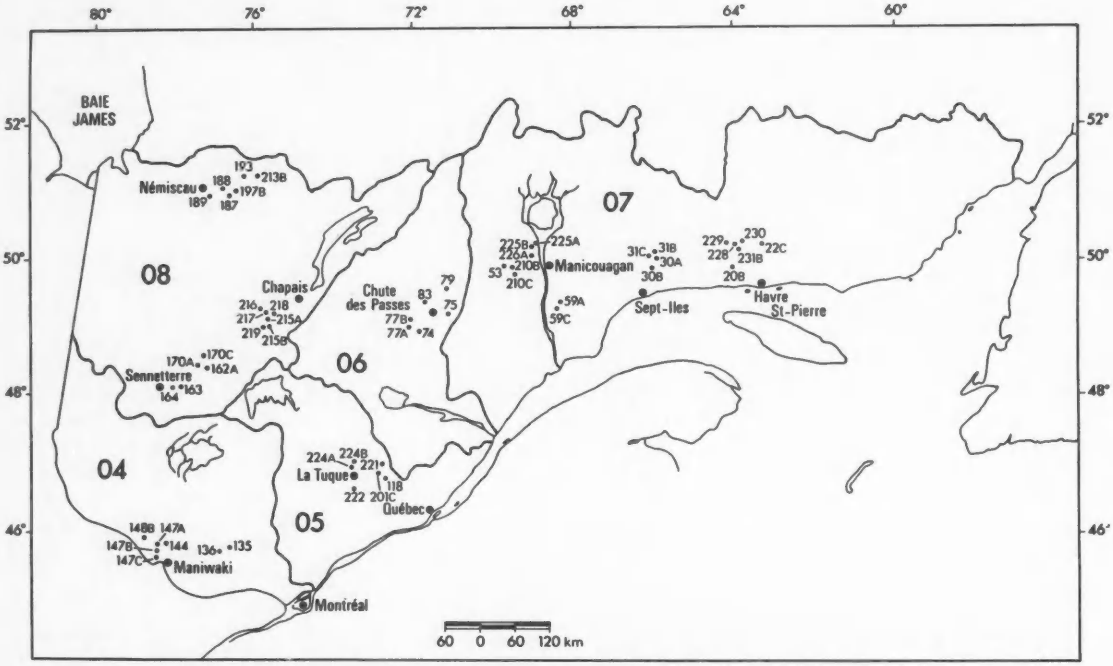

FIG. 1. Geographic location of study lakes in Quebec. Numbers refer to geographic region.

sampled exhibited alkalinity of less than 100 $\mu eq \cdot L^{-1}$ and had alkalinity to sulphate ratios below 1. Both parameters indicate an extreme sensitivity to acidification (Bobée et al. 1982).

Field and Laboratory Analysis

The field measurements were taken between August 11 and September 18, 1982. Morphometric data were computed for each lake from echo-sounder recordings. We derived lake morphometry data (area, maximum and mean depths, length, width) and watershed data (Table 1) from topographic maps at 1 : 50 000 scale. We calculated the morphoedaphic index (MEI; Ryder et al. 1984) from the ratio of conductivity to mean depth. Water sampling and preservation were performed following procedures established by Environment Canada (1979). Composite unfiltered water samples collected from the epilimnion (0–5 m) were used to determine water quality variables (Table 1) except that total organic carbon was measured in discrete samples taken just below the water surface. All analytical determinations were made according to methods described by Bobée et al. (1982). Alkalinity was determined by the Gran titration method (Kramer 1980). The alkalinity to sulphate ratio was also computed to evaluate the importance of the substitution of bicarbonate ions by sulphate ions within surface waters. This ratio indicates the degree of "anthropogenic acidification" (Bobée et al. 1982).

Zooplankton was sampled between July 9 and August 10, 1982. Samples were collected by means of a Wisconsin net (20.5 cm in diameter, 64-μm mesh) which was towed vertically from depths ranging from 2 to 20 m (63 – 628 L of filtered water; Pinel-Alloul and Codin-Blumer 1983). Zooplankton samples were preserved upon collecting in 9% formalin with sucrose (60 $g \cdot L^{-1}$, Prepas 1978). Laboratory procedures are described in Pinel-Alloul and Méthot (1984). Counts of zooplankters were expressed as numbers of individuals per cubic metre and were converted to biomass (milligrams per cubic metre) using the specific dry weights estimated by Pinel-Alloul and Méthot (1979) for the same species collected in the James Bay territory.

Statistical Analyses

The data consisted of 14 morphometric and 20 physicochemical variables plus density and biomass of 38 zooplankton species for each of the 54 study lakes. Statistical analyses were performed at the University of Montreal using the SPSS (Nie et al. 1975; Hull and Nie 1981) and R (Legendre and Vaudor 1984) packages of computer routines.

First, species present in less than 5% of the sampled sites were eliminated. Most of them were littoral or occasional species. This reduced the original data matrix to a final subset of 38 taxa. The data sets (abundance and biomass, respectively) were then transformed ($\ln (x + 1)$) to normalize the distribution of the variables and to achieve homoscedasticity. The transformed data matrix was then partitioned into groups of cooccurring species by means of a complete linkage cluster analysis (Legendre and Legendre 1979) based on the Gower similarity index. The Gower coefficient excludes double zeros (Legendre and Legendre 1979) and the complete clustering characteristically produces clusters of biological data that are functionally distinct from one another (Earle et al. 1987).

Morphometric, physical, and chemical data were also transformed ($\ln (x + 1)$; except pH) so as to normalize the abiotic data matrix and to give each variable a more equal weight in the analysis. Then, a factor analysis was performed to simplify the variance structure of these highly correlated and interdependent variables. This process resulted in orthogonally rotated (Varimax) factor scores, each factor representing an integrated environmental property correlated with a set of colinear abiotic variables.

The factor analysis also served to simplify the analysis of relationships between abiotic factors and zooplankton species which were investigated through correlation analysis between the factor scores and the abundance and biomass of each species using Spearman correlations. Furthermore, the use of Spearman correlations of species abundance with water temperature and dissolved oxygen at time of sampling also allowed us to test the effect of the season on zooplankton species estimates. A similar statistical approach was used with success by Earle et al. (1986, 1987) to analyse the factors influencing the distribution of phytoplankton in Labrador and Newfoundland lakes.

Group	Taxon	No. of lakes	pH	SO_4
1	DAPHNIA DUBIA	11	6.1	89
	LEPTODORA KINDTII	9	6.1	95
	TRICHOCERCA CYLINDRICA	22	6.1	75
	ASPLANCHNA PRIODONTA	13	5.8	88
	ROTIFER IND.	5	5.9	83
2	DAPHNIA SP.	10	5.9	85
	LEPTODIAPTOMUS SICILIS	8	6.1	99
	SIDA CRYSTALLINA	8	6.6	120
	CERIODAPHNIA RETICULATA	3	6.7	76
	TRICHOCERCA MULTICRENIS	5	5.6	96
	LEPTODIAPTOMUS ASHLANDI	3	6.2	63
3	GASTROPUS SP.	14	5.9	55
	SKISTODIAPTOMUS OREGONENSIS	5	7.1	88
	SYNCHAETA SP.	8	6.1	83
4	DAPHNIA ROSEA	15	6.1	62
	EPISCHURA LACUSTRIS	21	6.5	64
	DAPHNIA LONGISPINA	16	6.4	72
	KERATELLA HIEMALIS	13	6.0	67
	CYCLOPS SCUTIFER	21	5.9	59
	DAPHNIA SCHODLERI	25	6.0	73
5A	DIAPHANOSOMA SP.	17	6.5	112
	MESOCYCLOPS EDAX	21	5.5	97
	DIACYCLOPS BICUSPIDATUS THOMASI	19	6.4	86
	DAPHNIA GALEATA MENDOTAE	14	6.4	83
5B	KERATELLA QUADRATA	4	6.5	104
	FILINIA LONGISETA	3	7.1	139
	TROPOCYCLOPS PRASINUS	4	6.7	89
6	BOSMINA LONGIROSTRIS	43	6.0	73
	LEPTODIAPTOMUS MINUTUS	36	5.9	67
	KERATELLA TAUROCEPHALA	39	5.9	67
	HOLOPEDIUM GIBBERUM	41	6.0	72
	POLYARTHRA VULGARIS	42	6.2	80
7	DIAPTOMID COPEPODID	53	6.0	77
	NAUPLII	54	6.0	76
	KELLICOTTIA LONGISPINA	52	6.0	77
	KERATELLA COCHLEARIS	53	6.0	74
	CYCLOPOID COPEPODID	45	6.1	80
	CONOCHILUS SP.	41	6.0	64

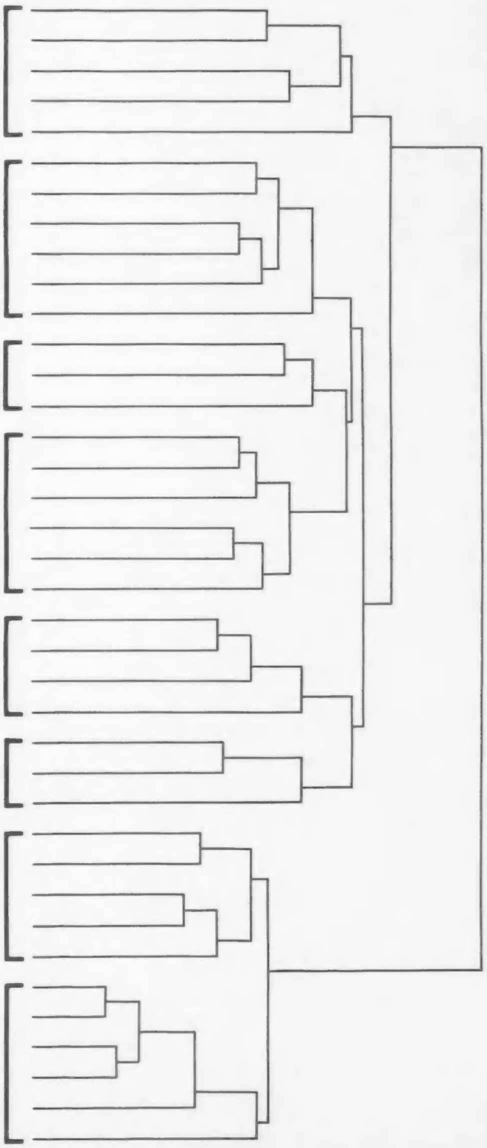

FIG. 2. Results of the complete linkage cluster analysis of zooplankton species based on their abundance in 54 lakes. The number of lakes and means of pH and sulphate concentrations ($\mu eq \cdot L^{-1}$) of the lakes in which the taxon occurred are also presented.

TABLE 2. Factor analysis of 34 physical, chemical, and morphometric variables. Correlation coefficients are between the seven derived factors and the 34 original variables. Nonsignificant coefficients (i.e. ⟨0.250; p ⟩0.05) have been omitted.

Variable	Factor 1: hardness–alkalinity	Factor 2: lake depth, water transparency	Factor 3: dystrophy, color	Factor 4: Lake size	Factor 5: salinity, sulphate	Factor 6: lake volume development	Factor 7: nitrate
Alkalinity	0.916	—	—	—	—	—	—
Alkalinity/sulphate ratio	0.912	—	—	—	—	—	—
Calcium	0.905	—	—	—	0.301	—	—
pH	0.901	—	—	—	—	—	—
Magnesium	0.873	−0.277	—	—	—	—	—
Hydrogen	−0.754	—	—	—	—	0.367	—
Conductivity	0.731	—	—	—	0.411	—	—
Potassium	0.600	—	—	—	0.581	—	—
Zinc	−0.512	—	0.447	—	—	—	—
Maximum depth	—	0.929	—	—	—		—
Lake relative depth	—	0.919	—	—	—	—	—
Lake mean depth	—	0.863	—	—	—	—	—
Morphoedaphic index	0.518	−0.693	—	—	0.301	0.274	—
Volume	—	0.685	—	0.621	—	—	—
Manganese	−0.323	−0.642	—	—	—	—	0.417
Longitude	0.309	−0.605	—	−0.285	0.492	—	—
Dissolved organic carbon	—	—	0.904	—	—	—	—
Total organic carbon	—	—	0.899	—	—	—	—
Color	—	—	0.723	—	−0.476	−0.329	—
Chlorine	—	—	0.682	—	—	−0.322	−0.271
Iron	—	−0.554	0.652	—	—	—	—
Secchi disk	—	0.600	−0.640	—	—	—	—
Total aluminium	−0.549	—	0.556	—	−0.422	−0.250	—
Lake order	—	0.416	0.528	0.293	—	0.270	0.298
Lake area	—	—	—	0.926	—		—
Maximum length	—	—	—	0.842	—	—	—
Maximum width	—	—	—	0.806	—	—	—
Watershed area	—	0.375	0.470	0.654	—	—	—
Sodium	—	—	—	—	0.797	—	−0.302
Sulphate	0.376	—	—	−0.283	0.769	—	0.259
Latitude	−0.442	—	—	—	−0.617	—	−0.335
Lake volume development	—	−0.433	—	—	—	—	—
Altitude	−0.379	−0.270	—	—	−0.363	0.722	—
Nitrate	—	—	—	—	—	−0.594	0.763
Eigenvalue	7.218	5.674	4.671	3.720	3.438	1.727	1.615
Percentage of variance	21.23	16.69	13.74	10.94	10.11	5.08	4.75

Results

Species Associations

Fifty-three zooplankton taxa were identified from the 54 lakes examined in this study, including the copepodid and the naupliar stages. An average of 13 taxa per sample was found, ranging from 8 to 19. Many species were present in more than 66% of the lakes (Fig. 2). The most ubiquitous species were *Keratella cochlearis, Kellicottia longispina, Bosmina longirostris*, and *Polyarthra vulgaris*. The zooplankton density varied between 7720 and 240 423 ind·m^{-3} (Pinel-Alloul and Méthot 1985).

The dendrogram from the complete linkage cluster analysis (Fig. 2) suggests that the zooplankton communities in Quebec lakes can be partitioned into eight different species associations and subgroups ($p < 0.05$). Results from Kruskall–Wallis tests (Siegel 1956) showed that mean pH of the lakes from which they came did not vary significantly from one species group to another ($p > 0.05$) but sulphate concentrations varied significantly among the species associations ($p < 0.01$). However, general trends could be detected from bivariate Mann–Whitney tests (Siegel 1956) on differences in mean pH or sulphate concentrations between pairs of species associations. Species from groups 1, 6, and 7 occurred in the most acidic lakes with a mean pH below 6.2. Group 5B represented zooplankton species characteristic of the circumneutral lakes. Species from groups 6 and 7 seemed to be characteristic of lakes with a low sulphate concentration. Species of groups 1, 2, 3, 5A, and 5B were found in lakes where the mean sulphate concentration was generally high; group 5B associated with the highest level (89–139 μeq·L^{-1}).

Environmental Factors

The factor analysis on the abiotic variables shows that 82% of the total variance can be explained by the first seven derived factors (Table 2). Factor 1 explained 21% of the total variance and was positively correlated with alkalinity, alkalinity to sulphate ratio, calcium, pH, magnesium, conductivity, potassium, and the morphoedaphic index and was negatively correlated with hydrogen ion, total aluminium, and zinc. It is considered a hardness–alkalinity factor. Factor 2, which explained 17% of the variance, was positively correlated with depth and volume morphometric variables and with water transparency. It is thus considered a lake depth and water transparency factor. It was also negatively related to the morphoedaphic index, manganese, longitude, and iron. Factor 3, responsible for 14% of the variance, was positively correlated with dissolved organic carbon, total organic carbon, color, chlorine, iron, total aluminium, and lake order. It represents a dystrophy factor. Factor 4 explained 11% of the variance and was positively correlated with area, width, length, watershed area, and volume of lakes, which made it a lake size factor. High positive loading by sodium and sulphate on factor 5 indicated a salinity–sulphate factor. This factor was also associated with low latitude. Factor 6, positively associated with lake volume development and negatively correlated with altitude, represents the lake shape. Factor 7 was correlated with nitrate.

Relationships between Zooplankton Species or Associations and Environmental Factors

Table 3 shows correlations between zooplankton species abundances or associations and the derived environmental factors. Most species were significantly related to at least one of the factors ($p < 0.05$).

A few species were strongly correlated with factor 1 (alkalinity–hardness), especially *Daphnia galeata mendotae, Mesocyclops edax, Diacyclops bicuspidatus thomasi*, and *Diaphanosoma* sp., all group 5A species. Species from group 6 showed a negative correlation with factor 1, particularly *Keratella taurocephala, Bosmina longirostris*, and *Holopedium gibberum*.

Only a small number of species, all from groups 4 and 5B, were positively correlated with factor 2 (lake depth and water transparency), especially *Cyclops scutifer, Keratella hiemalis, Daphnia schodleri*, and *Keratella quadrata*. On the other hand, all other species associations had representatives that were negatively associated with factor 2: *Trichocerca cylindrica, Polyarthra vulgaris*, and *Leptodiaptomus minutus* having the highest degree of negative correlation.

Only a few species were correlated with factor 3 (dystrophy), some positively: *Ceriodaphnia reticulata* from group 2 and *Daphnia rosea* and *Epischura lacustris* from group 4.

Factor 4 (lake size) also showed few significant correlations with any species. Positive correlations were noted with *Leptodiaptomus ashlandi* from group 2 and *Conochilus* sp. from group 7. A negative correlation was observed with *Tropocyclops prasinus* in group 5B.

Many zooplankters were positively associated with factor 5 (salinity–sulphate): included are *Sida crystallina, Diaphanosoma* sp., *Asplanchna priodonta, Leptodiaptomus sicilis, Mesocyclops edax, Filinia longiseta, Polyarthra vulgaris*, and the cyclopoid copepodids. These taxa belonged to groups 1, 2, 5 (A and B), 6, and 7. Negative correlations with factor 5 were noted for *Gastropus* sp., *Cyclops scutifer, Leptodiaptomus minutus*, and *Conochilus* sp.

The majority of the species positively associated with factor 6 (lake volume development) belonged to groups 6 and 7, *Bosmina longirostris, Leptodiaptomus minutus*, and *Keratella cochlearis* showing the strongest correlations. Species that were negatively related to this factor were from group 4, including *Daphnia rosea, D. longiremis*, and *D. schodleri*. *Asplanchna priodonta, Trichocerca multicrenis*, and *Keratella quadrata* in groups 1, 2, and 5B also showed preferences for lakes with greater lake volume development index.

A few species were positively related to factor 7 (nitrate), notably *Asplanchna priodonta, Trichocerca multicrenis*, and *Diaphanosoma* sp. Negative correlations with this factor were noted for *Epischura lacustris, Leptodiaptomus minutus*, and *Conochilus* sp.

To evaluate seasonality effects on zooplankter abundances, we calculated the correlations between species abundances, water temperature, and dissolved oxygen at the time of sampling (Table 3). Some species presented a significant correlation with one of the seasonality factors. Among the warmwater species were *Diaphanosoma* sp., *Sida crystallina, Filinia longiseta, Mesocyclops edax, Keratella quadrata*, and *Trichocerca multicrenis*. Coldwater species consisted of *Conochilus* sp., *Leptodiaptomus minutus, Cyclops scutifer*, and *Epischura lacustris*. Few relations were obtained with dissolved oxygen. *Conochilus* sp. and *Leptodiaptomus minutus* were associated with well-oxygenated waters. Inverse relations were noted for *Ceriodaphnia reticulata, Daphnia rosea*, and *Diaphanosoma* sp.

Correlations between the species groups, considered as a whole, and the derived environmental factors were also calculated (Table 3). Group 1 was negatively correlated with the lake depth and water transparency factor, the dystrophy factor, and the lake size factor. Group 2 was positively correlated with the salinity–sulphate factor and group 3 showed the inverse pattern. Group 4 was positively correlated with the dystrophy factor and negatively correlated with the lake volume development factor. Group 4 also contained the coldwater species association. Group 5A was positively correlated with the alkalinity–hardness and salinity–sulphate factors; it was negatively associated with the lake depth and water transparency factor. Inversely, group 5B was positively correlated with the lake depth and water transparency factor. Group 6 was negatively correlated with the alkalinity–hardness factor and the lake depth and water transparency factor. It was positively associated with the lake volume development factor. Group 7 was negatively correlated with the lake depth and water transparency factor and positively related to the lake volume development factor.

The correlation analysis between zooplankton species estimates expressed as biomass and the derived environmental factors gave similar results to those obtained for species abundances. However, except for group 5A, the species associations were not quite the same in biomass and in abundance. Associations based on biomass gathered together species of the same weight rather than species with identical numerical importance.

Zooplankton Size and Trophic Structures in Relation to pH

The community structure, whether expressed in size classes (Fig. 3A) or in trophic groups (Fig. 3B), tended to vary among sets of lakes of different pH. Assignment of species to size classes was based on specific mean length and followed Roff et al. (1981) categories. In more acidic lakes, most of the community was represented by small organisms (<0.99 mm; rotifers, small crustaceans). In neutral lakes, all size classes were represented and there was an increase of large plankters. In more alkaline lakes, small plankters were again dominant.

TABLE 3. Spearman correlation coefficients between the seven derived factors and the abundances of selected zooplankton species. Species taxa are grouped according to the results of the clustering analysis. Significant correlations: $*p \leq 0.05$; $**0.05 \langle p \leq 0.01$; $***0.01 \langle p \leq 0.001$.

Species	T°	DO	Factor 1: hardness alkalinity	Factor 2: lake depth, water transparency	Factor 3: dystrophy, color	Factor 4: lake size	Factor 5: salinity, sulphate	Factor 6: lake volume development	Factor 7: nitrate
Group 1									
Trichocerca cylindrica	—	—	—	−0.5***	—	—	—	—	—
Asplanchna priodonta	—	—	−0.2*	—	—	—	0.3*	0.3**	0.3*
Rotifer ind.	—	—	−0.3*	—	—	—	0.3*	—	—
Daphnia dubia	—	—	—	—	—	—	0.2*	—	—
Leptodora kindtii	—	—	—	—	—	—	—	—	—
Group	—	—	—	−0.4**	−0.3*	−0.3*	—	—	—
Group 2									
Daphnia sp.	—	—	—	—	—	—	—	—	—
Leptodiaptomus sicilis	0.2*	—	—	—	—	—	0.3*	—	—
Sida crystallina	0.4**	—	—	—	—	—	0.4**	—	—
Ceriodaphnia reticulata	—	−0.3*	—	−0.2*	0.3**	—	—	—	—
Trichocerca multicrenis	0.3*	—	−0.3*	—	—	—	—	0.3*	0.3**
Leptodiaptomus ashlandi	−0.2*	—	—	−0.3*	—	0.3*	—	—	—
Group	—	—	—	—	—	—	0.4**	—	—
Group 3									
Gastropus sp.									
Skistodiaptomus	—	—	—	—	—	—	−0.3*	—	—
oregonensis	0.2*	—	0.2*	—	—	—	—	—	—
Synchaeta sp.	—	—	—	—	—	—	—	—	—
Group	—	—	—	—	—	—	−0.3*	—	—
Group 4									
Daphnia rosea	—	−0.3*	—	—	0.3*	—	—	−0.3*	—
Epischura lacustris	−0.3*	—	—	—	0.3*	—	—	—	−0.3*
Daphnia longiremis	−0.2*	—	—	—	—	—	—	−0.3**	—
Keratella hiemalis	—	—	—	0.4***	—	—	—	—	—
Cyclops scutifer	−0.4**	—	—	0.5***	—	—	−0.4**	—	—
Daphnia schodleri	—	—	—	0.3*	—	—	—	−0.3*	—
Group	−0.3*	—	—	—	0.3*	—	—	−0.3*	—
Group 5A									
Diaphanosoma sp.	0.5***	−0.2*	0.3**	—	—	—	0.4**	—	0.3*
Mesocyclops edax	0.3*	—	0.5***	—	—	—	0.3*	—	—
Diacyclops bicuspidatus thomasi	—	—	0.3**	−0.3*	—	—	—	—	—
Daphnia galeata mendotae	—	—	0.6***	—	—	—	—	—	—
Group	—	—	0.5***	−0.4***	—	—	0.2*	—	—
Group 5B									
Keratella quadrata	0.3*	—	—	0.2*	—	—	—	0.3*	0.2*
Filinia longiseta	0.4**	—	0.3*	—	—	—	0.3*	—	—
Tropocylcops prasinus	—	—	—	—	—	−0.3*	—	—	—
Group	0.3*	—	—	0.2*	—	—	—	—	—
Group 6									
Bosmina longirostris	—	—	−0.4**	—	—	—	—	0.6***	—
Leptodiaptomus minutus	−0.4***	0.3*	—	−0.4**	—	—	−0.3*	0.4***	−0.3*
Keratella taurocephala	—	—	−0.8***	−0.3*	—	—	—	—	—
Holopedium gibberum	—	—	−0.2*	—	—	—	0.2*	—	−0.2*
Polyarthra vulgaris	—	—	—	−0.5***	—	—	0.3*	—	—
Group	—	—	−0.5***	−0.5***	—	—	—	0.4***	—
Group 7									
Diaptomid copepod	—	—	—	−0.3*	—	—	—	—	0.2*
Nauplii	—	—	—	−0.5***	—	—	—	—	—
Kellicottia longispina	—	—	—	−0.2*	—	—	—	—	—
Keratella cochlearis	—	—	—	—	—	—	—	0.4**	—
Cyclopoid copepodid	—	—	0.4**	—	—	—	0.3*	—	—
Conochilus sp.	−0.6***	0.4**	—	—	—	0.3*	−0.3*	—	−0.4**
Group	—	—	—	−0.5***	—	—	—	0.2*	—

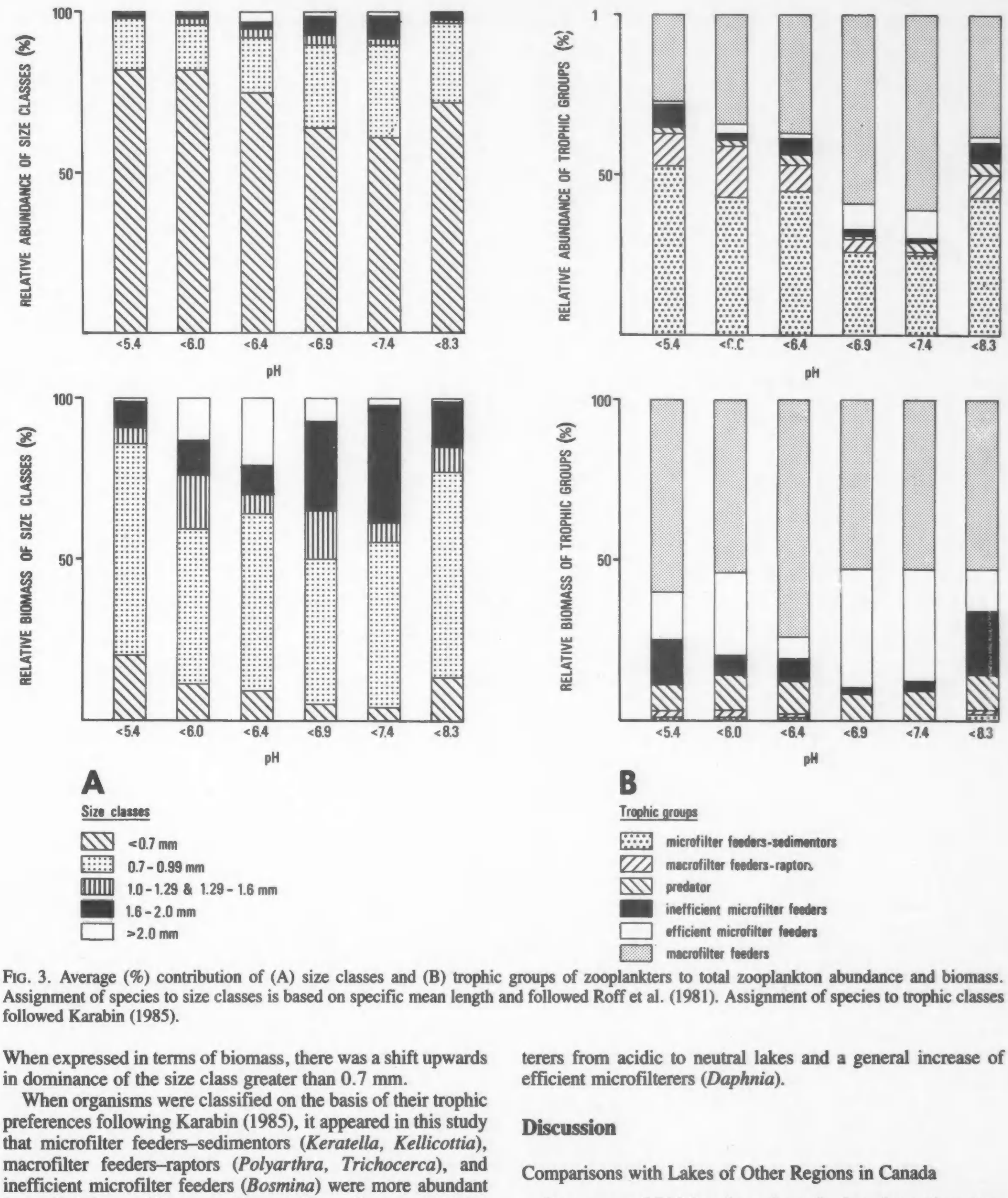

FIG. 3. Average (%) contribution of (A) size classes and (B) trophic groups of zooplankters to total zooplankton abundance and biomass. Assignment of species to size classes is based on specific mean length and followed Roff et al. (1981). Assignment of species to trophic classes followed Karabin (1985).

When expressed in terms of biomass, there was a shift upwards in dominance of the size class greater than 0.7 mm.

When organisms were classified on the basis of their trophic preferences following Karabin (1985), it appeared in this study that microfilter feeders–sedimentors (*Keratella, Kellicottia*), macrofilter feeders–raptors (*Polyarthra, Trichocerca*), and inefficient microfilter feeders (*Bosmina*) were more abundant in acidic lakes, while macrofilterers (*Leptodiaptomus, Holopedium, Sida*) and efficient microfilters (*Daphnia*) dominated in neutral lakes. In more alkaline lakes, 50% of the zooplankton consisted of small microfilters–sedimentors and macrofilters–raptors (Fig. 3B). The results expressed in terms of contribution to total biomass showed a decline of microfilter feeders–sedimentors, macrofilter feeders–raptors, and inefficient microfilterers from acidic to neutral lakes and a general increase of efficient microfilterers (*Daphnia*).

Discussion

Comparisons with Lakes of Other Regions in Canada

Our survey of 54 lakes throughout Quebec shows that water chemistry is variable among lakes (Table 1). Comparisons with other surveys done in Quebec lakes by Kelso et al. (1986) and Lachance et al. (1984) using the same sets of variables (Table 4) indicate that our lake sample can be considered representative of the variability of Quebec lakes for most of the morphometric characteristics with a bias toward larger lake size. Ranges of

TABLE 4. Comparison of morphometric, physical, and chemical characteristics of sampled lakes in Quebec. Mean (range); N = number of lakes in each data set.

Characteristic	Kelso et al. (1986)	Lachance et al. (1984), Canadian Shield	Present study, Canadian Shield
N	251	199	54
Morphometric			
Lake area (ha)	147 (12–1784)	(10–1300)	208.4 (36–721)
Maximum depth (m)	17.5 (1.0–90.0)	(0.5–10)	21.1 (4–83)
Watershed area (ha)	2534 (78–53 192)		3855.5 (261–29 843)
Elevation (m)	403 (30–920)		362.1 (76–655)
Physical and Chemical			
pH	6.54 (4.71–8.38)	5.2 (4.0–8.0)	6.0 (5.2–8.3)
Alkalinity ($\mu\mathrm{eq}\cdot\mathrm{L}^{-1}$)	124.6 (0–1607)	66 ± 162	107.5 (1–585)
Conductivity ($\mu\mathrm{S}\cdot\mathrm{cm}^{-1}$)	25.6 (5–185)	27 ± 20	22.3 (6–130)
Total organic carbon ($\mathrm{mg}\cdot\mathrm{L}^{-1}$)	6.1 (1–15)	12 ± 4	6.1 (3–11)
Dissolved organic carbon ($\mathrm{mg}\cdot\mathrm{L}^{-1}$)	3.3 (1–16)		5.9 (2–11)
Ca ($\mathrm{mg}\cdot\mathrm{L}^{-1}$)	134.6 (15.9–1437.1)	141 ± 154	125.6 (16–678.6)
Mg ($\mathrm{mg}\cdot\mathrm{L}^{-1}$)	51.3 (6.2–516.5)	50 ± 30	43.4 (6.3–225.3)
Na ($\mathrm{mg}\cdot\mathrm{L}^{-1}$)	25.5 (8.2–54.8)	30 ± 18	24.3 (11.3–46.1)
SO_4 ($\mathrm{mg}\cdot\mathrm{L}^{-1}$)	77.9 (20.8–229.1)	104 ± 33	76.4 (20–229)
Al ($\mu\mathrm{g}\cdot\mathrm{L}^{-1}$)	90.4 (7.2–299.5)	108 ± 87	104.5 (14–228)
Mn ($\mu\mathrm{g}\cdot\mathrm{L}^{-1}$)	10.8 (0–41.2)	17 ± 15	11.8 (1–40)

pH, alkalinity, conductivity, organic carbon, and ions from our data are similar to those of the larger sample of Quebec lakes analysed by Kelso et al. (1986), despite the absence of lakes with pH lower than 5 in our sample. Comparisons between our sample and that of Lachance et al. (1984) consisting of 199 Canadian Shield lakes indicate a bias toward higher alkalinities, higher pH, and lower levels of organic carbon and sulphate in our lake sample (Table 4).

Lakes Characteristics and Acidification

Five environmental composite factors (Table 2) account for the most discriminant abiotic characteristics of our lakes. The distribution pattern of acidity or alkalinity represents the major feature in water chemistry, but lake morphometry also accounts for the observed environmental variability.

Natural acidity, as expressed by the hydrogen ion and levels of metal contamination (zinc, aluminum, and manganese), has a significant negative loading on the first factor (alkalinity–hardness) and is related to lakes at higher altitude in the northeastern regions of Quebec. Higher pH is associated with the alkalinity–hardness factor along with calcium, magnesium, conductivity, and levels of sulphate and is related to lakes that are situated in southwestern Quebec. To estimate anthropogenic acidification of lakes in Quebec, we have to consider sulphate and metal concentrations. High loading of sulphate on factor 5 reveals the importance of the process. The factor analysis also shows that in our lake sample, the atmospheric deposition of sulphates has not yet resulted in a substantial reduction of pH, since the majority of lakes affected are well buffered by high calcium content.

According to Bobée and Lachance (1984) and Pinel-Alloul et al. (1987), Quebec lakes can be classified in relation to acidification processes. Vulnerability or sensitivity to acidification depends on the water mineralisation indicated by calcium, magnesium, and conductivity values. Anthropogenic acidification is related to the sulphate content of lakes, and natural acidity depends on hydrogen ion levels (pH) and buffered capability (alkalinity). Our study showed that regions with high vulnerability were located on the north shore of the St. Lawrence River and in the Parc des Laurentides; the least vulnerable zones were situated in midwestern Quebec (La Tuque and Lac St-Jean regions), and lakes with low vulnerability were located in regions affected by acid precipitation with high sulphate values and high mineralisation levels (Maniwaki region). Although this last region was considered by J. Dupont (pers. comm.) as enriched in sulphate by the high levels of pyrite in the soil, the high sulphate concentrations (mean of 76.4 $\mu\mathrm{eq}\cdot\mathrm{L}^{-1}$) (Table 1) in our lakes might be attributed to anthropogenic acidification (Bobée et al. 1982; Lachance et al. 1984). Lakes with more than 60 μeq sulphate$\cdot\mathrm{L}^{-1}$ are considered to be impacted by acid precipitation even when their alkalinity and mineralisation are high (Harvey et al. 1981).

As indicated by the factors 2 and 4, morphometric features also play an important role in lake typology (Table 2). Deeper lakes of large volume are situated in the eastern regions at low altitude; they show transparent waters as suggested by the loadings of the Secchi disk on factor 2. Factor 3 shows evidence of dystrophic influence in lakes of greater hydrologic order.

Zooplankters Responses to Environmental Factors

Our study showed that many factors in addition to acidification served to determine the zooplankton communities of Quebec lakes. Furthermore, although not evaluated in the present study, the distribution of zooplankton species might depend also on biological factors such as trophy (Pinel-Alloul et al. 1987) and predation and competition (Kerfoot 1987; Kerfoot and Sih 1987).

The majority of species belonging to group 5A (Fig. 2) were linked to the hardness–alkalinity factor. These species were likely to occur most prominently in lakes of the western region of Quebec: Maniwaki, La Tuque, and Chapais (Pinel-Alloul and Méthot 1985). *Bosmina longirostris, Leptodiaptomus min-*

utus, Keratella taurocephala, and Polyarthra vulgaris, and *Holopedium gibberum* represented the acid-tolerant species (group 6; Fig. 2); the first two were found in eastern and western parts of the sampling area, and the rotifers were dominant mainly in the western regions (Pinel-Alloul and Méthot 1985).

The examination of trends in the occurrence and abundance of zooplankton species in relation to the acidity–alkalinity continuum yielded ambiguous results. Many authors reported different species associations for acidic or nonacidic lakes, but most of the dominant species in eastern Canadian lakes have an ubiquitous nature. *Mesocyclops edax, Leptodiaptomus minutus, Holopedium gibberum, Diacyclops bicuspidatus thomasi*, and *Diaphanosoma leuchtenbergianum* are listed as species occurring over a large range of pH (Carter et al. 1980; Confer et al. 1983). *Bosmina longirostris*, generally documented as a common inhabitant of acidic lakes (Sprules 1975; Roff and Kwiatkowski 1977; Malley and Change 1986; Pinel-Alloul et al. 1987), also occurs as a dominant species over a large range of pH (Yan and Strus 1980; Keller and Pitblado 1984). However, North American lakes with low pH are often numerically dominated by *Bosmina longirostris* and *Leptodiaptomus minutus* (Yan and Strus 1980). On the contrary, *Diaphasonoma* sp. and *Daphnia galeata mendotae* are reported to be intolerant to acidity (Roff and Kwiatkowski 1977; Malley and Chang 1986; Pinel-Alloul et al. 1987; Bruns and Wiersma 1988). Cluster analyses of zooplankton communities in Quebec lakes support these generalities on species distribution in relation to pH (Table 3) with few exceptions. Hence, *Holopedium gibberum*, considered in our study as an acid-tolerant species, is reported over a wide range of pH (Confer et al. 1983) and in calcium-deficient water of the temperate Holarctic (Hutchinson 1967). But it is also categorized as tolerant to acidification (Sprules 1975; Roff and Kwiatkowski 1977; Pope et al. 1985; Havas and Likens 1985; Bruns and Wiersam 1988; present study). Within the acid-tolerant rotifers, *Keratella taurocephala* is a sporadic species in the Great Lakes, but commonly occurs in acid bogs or lakes of low conductivity, and *Polyarthra vulgaris* is a dominant species in the Great Lakes (Stemberger 1979).

The mechanisms responsible for the size structure of zooplankton communities in acidic lakes remain unclear even though the general trends towards the increasing importance of smaller taxa and lower abundance are apparent in many studies (Confer et al. 1983; Keller and Pitblado 1984; Kelso et al. 1986; Pinel-Alloul et al. 1987; present study). Community changes in size structure may imply direct toxicity by acid and metal contamination (Malley and Chang 1986), indirect cascading effects of changes in phytoplankton or fish communities (Kerfoot 1987), and reduced competition by large cladocerans (DeMott and Kerfoot 1982; Goulden et al. 1982). Trophic structure of zooplankton communities is also related to the acidification process. Keller and Pitblado (1984) observed a reduction of daphnids concomitant with an increase in the abundance of small grazers (*Leptodiaptomus minutus*) and a decrease in abundance of predators in more acidic lakes. Our results were similar to theirs when expressed in terms of biomass because these authors considered only crustaceans in their study and rotifers represented an important fraction of the total zooplankton density but not biomass. Compared with daphnids, *Bosmina longirostris* is an "inefficient" microfilter–feeder (Karabin 1985); its optimum food particle size is below 2–5 µm and its diet is therefore dominated by microplankton, bacteria, and detritus (Gliwicz 1977). The increased importance of cladoceran grazers such as *Bosmina longirostris* and *Holopedium gibberum* in acidic lakes suggests a reduction in competition from daphnids which are less tolerant to acidification.

The morphometric and light penetration features of lakes also influence the distribution of zooplankton species or groups (Table 3). Most species were negatively related to the second factor (lake depth and water transparency). Deep lakes situated in eastern Quebec harboured few species (Pinel-Alloul et al. 1987) and most species seemed to prefer shallow lakes, except some representatives from groups 4 and 5B. *Daphnia rosea, D. longiremis, Keratella hiemalis, Cyclops scutifer*, and *Daphnia schodleri* were found in deep and clear lakes or/and lakes with convex slopes and showed positive correlations with factor 2 (lake depth and water transparency) and/or negative correlations with factor 6 (lake volume development). These species occurred mainly in eastern Quebec: Havre St-Pierre, Sept-Îles, and Manicouagan (Pinel-Alloul and Méthot 1985). Some of these species (*Daphnia longiremis* and *Cyclops scutifer*) were coldwater organisms (Table 3). Similar thermal preferences were noted by Brooks (1957) and Carter et al. (1980). The rotifer *Keratella hiemalis* was also categorised as a coldwater form (Hutchinson 1967). Such a preference for deep lakes was rather unexpected for *Daphnia schodleri* which occurred in a wide spectrum of habitats and was principally a lake dweller confined to small lakes (Brandlova et al. 1972). This discrepancy might be related to the taxonomic difficulties encountered in the discrimination between *Daphnia rosea* and *D. schodleri*.

Only a few species (*Daphnia rosea* and *Epischura lacustris* from group 4 and *Ceriodaphnia reticulata* from group 2) demonstrated positive correlations with the dystrophy factor (factor 3). These species occurred in lakes situated in midwestern Quebec (Pinel-Alloul and Méthot 1985). These preferences seemed peculiar, since either *Epischura lacustris* or *Daphnia* sp. was not usually found below a pH of 5 (Confer et al. 1983). However, *Epischura lacustris* was tolerant to all extreme conditions of lake morphometry, water temperature, or water chemistry (Carter et al. 1980). *Ceriodaphnia*, usually found in weedy littoral regions of lakes or weedy pools (Brandlova et al. 1972), was better adapted to humic lakes. According to Gannon and Stemberger (1978), no crustacean plankters are strictly confined to dystrophic lakes and can be used as indicators.

Few species were related to lake size (factor 4). The large calanoid *Leptodiaptomus ashlandi* and the rotifer *Conochilus* sp. seemed to prefer large lakes, while *Tropocyclops prasinus* occurred in small lakes. According to Patalas (1972), the former was found associated with *Leptodiaptomus sicilis* in large oligotrophic Lake Superior. *Conochilus* sp. has been one of the most frequently encountered rotifers following the impoundment of northern Quebec reservoirs (Pinel-Alloul et al. 1989). This species was classified as a detritus bacterial feeder (Karabin 1985). Although it was found in large lakes, its presence can be better associated with the trophic status of the lake than with its size.

The majority of zooplankters were positively correlated with factor 5 (salinity–sulphate), particularly species belonging to groups 1, 2, and 5A. As discussed previously, the latter group of species was also related to the hardness–alkalinity factor. *Sida crystallina* and *Leptodiaptomus sicilis* occurred in hardwater lakes (Carter et al. 1980). *Leptodiaptomus sicilis* and *Daphnia dubia* had been found in larger, less productive Haliburton lakes (Sprules 1977). Species from group 1 included the rotifer *Asplanchna priodonta* previously reported by Fuller et al. (1977) from mesotrophic Douglas Lake. The majority of these species were found in lakes located in western Quebec:

Senneterre, Maniwaki, and La Tuque regions (Pinel-Alloul and Méthot 1985). Chlorine did not have any loading on factor 5 and all these lakes were far from the influence of sea spray. Hence, high sodium loading on factor 5 was difficult to interpret. *Gastropus* sp. and *Cyclops scutifer* were negatively related to the salinity–sulphate factor. The cyclopoid was already known to be absent from hardwater lakes (Carter et al. 1980).

Most of the species correlated with nitrates (factor 7) were positively so, except for some species from groups 4, 6, and 7. However, the very small fraction of the variance explained by this factor (4.75%) and the low value of the correlation coefficients did not allow us to infer zooplankton relationships with this variable.

Significant correlations between species abundances and the seasonality parameters, especially water temperature, might suggest that the distribution of zooplankton species in Quebec lakes was also related to their thermal preferences or their seasonal development. *Leptodiaptomus ashlandi, L. minutus, Epischura lacustris, Daphnia longiremis, Cyclops scutifer*, and *Conochilus* sp. were coldwater forms (Table 3) not found in southern U.S. lakes or found only in deep lakes (Carter et al. 1980). Most of the species positively related to temperature were the warm stenotherm *Filinia longiseta*, eurytherm *Keratella quadrata*, and *Trichocerca multicrenis* or midsummer species *Diaphanosoma* sp., *Sida cristallina*, and *Mesocyclops edax* (Hutchinson 1967; Stemberger 1979; Carter et al. 1980). In our study, seasonal development effects could be considered negligible because zooplankton sampling was performed in 1 mo. Hence, correlations between zooplankton species and water temperature should be interpreted in terms of geographic distribution brought about by temperature preferences.

Ecological Significance of Species Associations

The eight groups of species identified in the cluster analysis may be considered separate "species associations" characterized by distinct patterns of distribution. The species composing each of these associations cooccur because they have similar reactions to the environment. Correlations between species abundances and the seven derived environmental factors define the nature of individual zooplanktonic responses to abiotic conditions.

Our results show that groups of species demonstrate strong homogenous correlations with one of the seven derived environmental factors. For example, group 1 is an association of species which probably prefer small shallow dystrophic lakes rich in salts or sulphates. Group 2 represents species associated with shallow lakes with high levels of sulphate. Group 3 represents species found in lakes with low sulphate concentrations. Group 4 are coldwater species found in deep, dystrophic lakes. Group 5A is an association of hardwater species found in shallow lakes. Group 5B represents warm-water species found in deep lakes. Group 6 is the acid-tolerant association found in shallow lakes with high volume development. Group 7 are species found in more neutral shallow lakes.

Our study suggests that acidification patterns in Quebec lakes fail to account fully for the observed zooplankton species distributions. Additional factors related to morphometric features of lakes are also responsible for the observed spatial heterogeneity. The weakness of the relationships between zooplankton species and the abiotic environmental factors probably means that biotic factors might also generate heterogeneity in zooplankton community structure. Indeed, cascading indirect effects of acidification within the aquatic food web related to changes in competition, predation, or grazing patterns are not considered at all in this study. It is noteworthy that this paradigm is just becoming the base of the most recent studies on generative processes of zooplankton community structure (Kerfoot 1987; Kerfoot and Sih 1987).

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A Fur Seal Population Model Based on Age Structure Data

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Eberhardt, L. L. 1990. A fur seal population model based on age structure data. Can. J. Fish. Aquat. Sci. 47: 122–127.

About 16 000 female fur seals from the Pribilof Islands population were aged in pelagic collections from 1958 through 1974. A simple simulation model of the female population was used to vary population parameters until a minimum chi-square value was achieved for the fit of simulated annual age structures to those observed in the pelagic collection. Population trajectories resulting from either a diminishing reproductive rate or diminishing adult female survival rate approximated estimated pup population sizes, which were not used in developing the model, except that a subset of five observations was used to constrain model trajectories to the general neighborhood of the observed pup populations. The main finding of the study was that adult female survival rates varied sharply during the 1964 through 1974 period, after the major period of harvests of female fur seals. Further study of the age structure data may thus be useful in evaluating the poorly understood long-term reduction in abundance of Pribilof fur seals.

On a déterminé l'âge d'environ 16 000 phoques femelles appartenant à la population des îles Pribilof, capturées dans les eaux pélagiques de 1958 à 1974. On s'est ensuite servi d'un simple modèle de simulation de la population femelle pour varier les paramètres démographiques jusqu'à l'obtention d'une valeur minimum du chi-carré pour ajuster les courbes simulées de la structure annuelle des âges en fonction de celles observées chez les échantillons pélagiques. Les courbes démographiques obtenues d'une baisse du taux de reproduction ou du taux de survie des femelles adultes s'approchaient des tailles estimatives des effectifs de jeunes phoques qui n'ont pas servi à l'élaboration du modèle, sauf pour un sous-ensemble de cinq observations qui ont servi à limiter les courbes du modèle aux environs immédiats des populations observées de jeunes phoques. On a ainsi découvert que les taux de survie des femelles adultes ont nettement varié de 1964 à 1974, soit, après la principale période de chasse des phoques femelles. Une étude plus poussée des données sur la structure des âges pourrait donc permettre d'évaluer la baisse à long terme mal expliquée de l'abondance des phoques des îles Pribilof.

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One of the most extensive sets of data on a natural large mammal population is that for the Pribilof fur seal (*Callorhinus ursinus*). Nonetheless, there is presently no well-supported explanation for a persisting decline in abundance of the population. After a long history of over-exploitation, harvests were limited to young "bachelor" males and the population reached what is believed to be a relatively constant and maximum level in the early 1950's. In an effort to achieve a population level that would give a maximum sustainable yield, harvests of females began in 1956 and continued to 1968. Pup production declined about as expected, but then failed to increase significantly after cessation of the harvest of females, and has in fact continued to decline up to recent years.

From 1958 through 1974, rather extensive pelagic collections were made of adult female fur seals, with ages available for about 16 000 females over the 17-yr of the collections. In an earlier study of population dynamics of the Pribilof population (Eberhardt 1981), it was suggested that these age structure data could provide additional information about dynamics of the population. The present report suggests ways to further explore and exploit that data.

Materials and Methods

The approach of the present study depends on a simulation model similar to that of the earlier effort (Eberhardt 1981, p. 214–217), modified so that a number of parameters were varied in an effort to achieve a minimum chi-square fit of simulated age structure to that actually observed, using the tabulation of ages reported by York and Hartley (1981; table 2). Two versions of the model were used, one written in BASIC language, and employing nested program "loops" to range over possible parameter values in seeking the best chi-square fit to observed female age data. The calculations initially searched a wide range of parameter values for a minimum chi-square, using relatively large steps in the loops. In succeeding operations, the range of parameters searched over was narrowed and step sizes diminished accordingly. The second version employed a "spreadsheet" technique to provide a display of detailed data for any given set of parameters.

Two purposes were served by this dual approach, one being simply the opportunity to compare all of the simulated results with the actual data on age structure, harvests, and pup populations in a few pages of compressed output. Relevant portions could then readily be extracted and plotted for further study. The second purpose was that construction of two independent versions of the same model with quite different physical arrangements that served to identify errors in programming and to cross-check details of model structure.

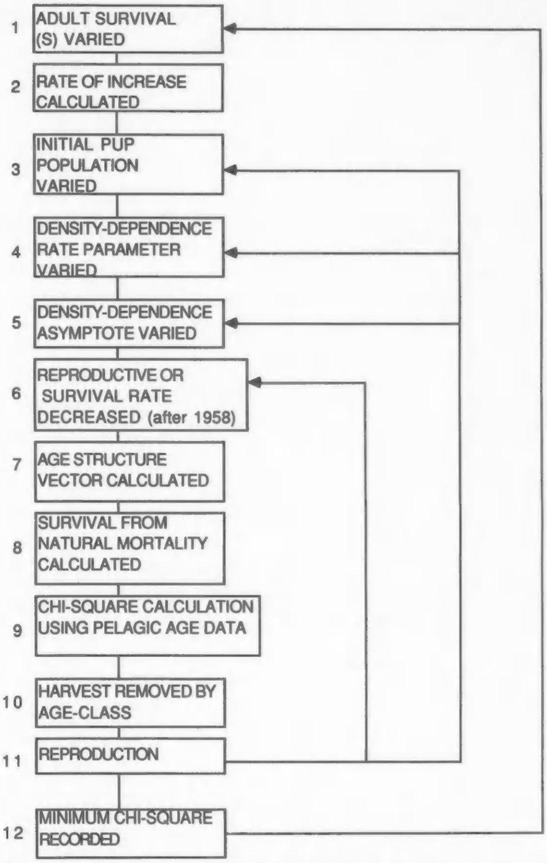
1
ADULT SURVIVAL (S) VARIED
2
RATE OF INCREASE CALCULATED
3
INITIAL PUP POPULATION VARIED
4
DENSITY-DEPENDENCE RATE PARAMETER VARIED
5
DENSITY-DEPENDENCE ASYMPTOTE VARIED
6
REPRODUCTIVE OR SURVIVAL RATE DECREASED (after 1958)
7
AGE STRUCTURE VECTOR CALCULATED
8
SURVIVAL FROM NATURAL MORTALITY CALCULATED
9
CHI-SQUARE CALCULATION USING PELAGIC AGE DATA
10
HARVEST REMOVED BY AGE-CLASS
11
REPRODUCTION
12
MINIMUM CHI-SQUARE RECORDED

FIG. 1. Structure of fur seal simulation model. Arrows denote program "loops" varied in the study. Further details are given in the text, keyed to numbers at left.

Structure of the simulation model (Fig. 1) follows the chronology of events in an annual cycle of Pribilof fur seal abundance. Various steps in the simulation are described below by numbers keyed to Fig. 1. Steps 1,3,4,5 and 6 are "for loops" ("do loops" in FORTRAN) that vary parameters in increments (step 6 was not used in initial calculations, where the reproductive and survival rates were assumed to remain constant throughout a given simulation). Several versions of the BASIC language program were used in initial explorations of the data. Another main loop (years) was required to make calculations for the 25 yrs of the study, as well as other subsidiary loops to accomplish the necessary age-specific computations at various stages.

The survivorship (l_x) and reproductive (m_x) functions were those described by Eberhardt (1985):

(1) $l_x = \exp[-a_1 - a_2 x - a_3(e^{b_3 x} - 1)]$

(2) $m_x = a[1 - e^{-b(x-c)}]\exp[-a_3(e^{b_3 x} - 1)]$

The m_x data used in the study were those used earlier (Eberhardt 1985; figure 5) to develop equation (2), with a (0.454) being mean reproductive rate (female births per female) of fully adult females, b (0.701) a rate parameter describing the rate of increase of reproductive rate from an initial age, c (3.97), while a_3 (0.000225) and b_3 (0.40) are senescence parameters. The same senescence parameters were used in equation (1) where $a_2 = -\log(S)$, with S the adult female annual survival rate, and a_1 is a parameter controlling early survivorship (from birth to age 1 here).

Early survival was assumed to depend on number of pups born, following the relationship used previously (Eberhardt 1981, p. 209–210), in which survival to age 1 was expressed as:

(3) $l_1 = S_o[1 - \exp\{-k(N_{\max} - N)\}]$

in which N denotes pup population size (only females were considered throughout the study) and S_0 is first year survival at lower population levels where density-dependence presumably has a negligible effect. S_0 was fixed throughout the study to give survival to age 3 as 0.40, as used in the earlier study. This was accomplished by calculating S_0 so that:

$$l_3 = S_0 S^2 = \exp(-a_1 - 3a_2) = 0.40,$$

where S is the current adult survival rate, which was varied in the simulations. Thus a_1 varies with a_2 to keep survival to age 3 (l_3) constant. $N_{\max}$ is an asymptotic pup population size while k controls the rate at which pup survival is reduced as the population approaches asymptotic size, and both are parameters varied in the study. The fourth parameter varied in the initial stage of the simulations is the initial pup population size (N_0) in 1950, which was used as starting date for the study. Harvests removed from the simulated population were those tabulated by Eberhardt (1981; table 4) from reports of the North Pacific Fur Seal Commission, and were recorded by age.

An initial stable age distribution (step 7) was determined from the "Lotka" equations discussed by Eberhardt (1985):

(4) $1 = \sum_{a}^{w} e^{-rx} l_x m_x$

(5) $c_x = B\, e^{-rx} l_x$,

where c_x is the proportion of age x and B is the multiplier needed to insure that the sum of the c_x is unity. Equation (4) is first solved for r, using l_x and m_x values from equations (1) and (2) and then the proportions (c_x) of various ages are calculated from equation (5) and applied to the initial population of females which is obtained by dividing the initial pup population (N_0) by c_o ($=B$). The minimum reproductive age used was $a = 4$, and the maximum age considered was $w = 25$. Note that the stable age distribution only serves as an initial condition; harvests were frequently selective of younger age females, so that a stable age distribution was not maintained.

The chi-square calculation on pelagic age structure data (step 9) was based on female seals aged 4 to 16, inasmuch as it seemed likely that ages younger than four were not adequately represented in the sample, and samples beyond age 16 were small enough in some years to have a disproportionate effect on calculated chi-squares (cf. table 2 of York and Hartley 1981). The chi-square calculation was:

$$\text{Chi-square} = \frac{(\text{observed} - \text{expected})^2}{\text{expected}},$$

with expected values obtained by multiplying the fraction of a given age class aged 4 through 16 in the model times the total aged 4 through 16 observed in the pelagic sample. When har-

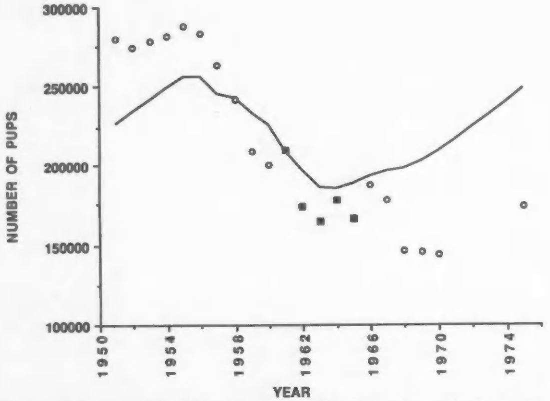

FIG. 2. Fit of model with constant reproductive and survival rates to observed data on pup population sizes. Solid points are those used to constrain model trajectories to the general neighborhood of estimates of pup population size.

vests greater than the available number in an age class of the simulated population were encountered in step 10, the program automatically discarded calculations for that particular "loop." In the final step (12) of Fig. 1, a variance based on comparison with actual estimated pup populations for 1961 to 1965 was calculated, using the pup population estimates of York and Hartley (1981; table 4) adjusted (by multiplying by 1.25) to compensate for the fact that only St. Paul pup populations were recorded there, and are about 80% of the total for the two Islands of the Pribilofs, as reported by York and Hartley (1981) and others. If the coefficient of variation of this variance exceeded 10%, the chi-square was not recorded. This was done to maintain the simulated populations in the neighborhood of populations actually estimated to be present. The 1961 to 1965 period was selected because pup populations began to be estimated in that period from direct field sampling using marked individuals by the method of Chapman and Johnson (1968). The criterion thus was:

$$\frac{\Sigma(\hat{N}_i - N_i)^2}{5\,\bar{N}^2} \leqslant 0.01.$$

Where the summation is over 1961 to 1965, $\hat{N}_i$ is population size from the model, and N denotes the observed pup population size.

The program described above is the main BASIC language program used in the study. Several variants were used to study subsets of the results (e.g. by "mapping" chi-square values for pairs of variables) and to print out details of calculations. The spreadsheet program followed the arrangement of Fig. 1, using single values of the parameters varied in the BASIC language program. It provided a printout of the complete age and harvest vectors, along with pelagic age structures, expected values, and individual chi-squares. The needed initial age structure was obtained from a separate "linked" spreadsheet which iterated to calculate r (from equation (4)) and the stable age structure of equation (5). Calculations were done on a Macintosh II microcomputer.

Results

When fixed reproductive rates ($a = 0.454$) were used, parameter estimates for minimum chi-square yielded a curve that failed to match the observed pup populations (Fig. 2). When pregnancy rates for ages 7–13 yr (Kajimura et al. 1979) are pooled over collecting areas, there is a distinct suggestion of a decrease in reproductive rate with time (Fig. 3). There is, however, an irregular pattern in distribution of collections over the years, which complicates interpretation of the data. The only area in which some collections were made in nearly all of the years of record was off the coasts of British Columbia, Washington, and Oregon. The results there are much more ambiguous as to change in reproductive rate over time (Fig. 3). Data from 1973 and 1974 was not used here because collections were made in the immediate vicinity of the Pribilofs and thus were distinctly biased towards pregnant females.

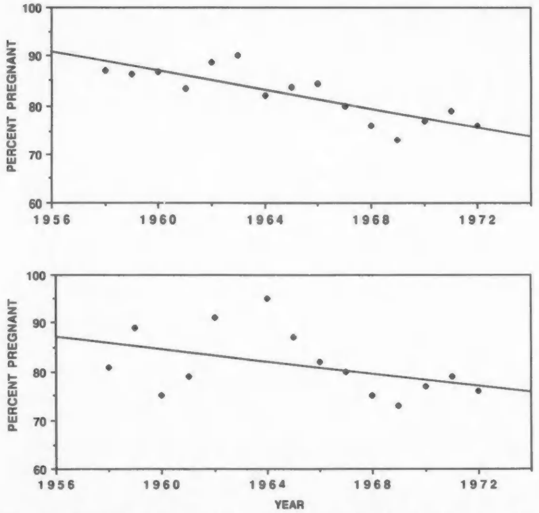

FIG. 3. Pregnancy rates (ages 7–13) from pelagic collections. Upper panel shows data pooled over all areas other than the immediate neighborhood of the Pribilof Islands, while lower panel shows data from the area off the coasts of British Columbia, Washington, and Oregon (the only area with collections in nearly all years).

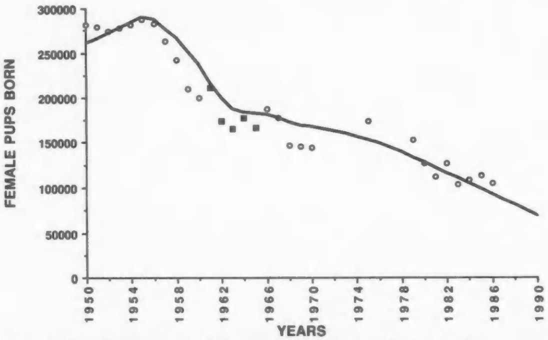

FIG. 4. Female pup populations from model with diminished reproduction after 1958 compared with actual estimates. Line shows pup population trend from model fitted to 1958–74 female age structure data by minimum chi-square method. Solid points represent years (1961–65) used to constrain chi-square fit to neighborhood of estimated pup population size. Estimates denoted by open symbols were not used in fitting model. Parameters giving minimum chi-square were $S = 0.934$, $N_0 = 260\ 000$, $k = 0.08$, $N_{max} = 300\ 000$ and $\Delta = 0.008$.

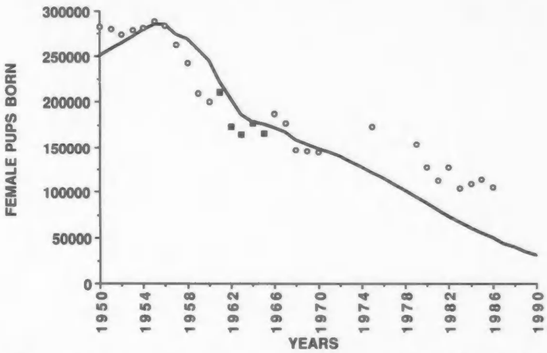

FIG. 5. Female pup populations from model with diminished adult female survival after 1958 compared with observed pup populations. As in Fig. 4, only the solid points have any influence in fitting the model. Parameters giving minimum chi-square were $S=0.94$, $N_0=250\,000$, $k=0.06$, $N_{max}=300\,000$, and $\Delta=0.0052$.

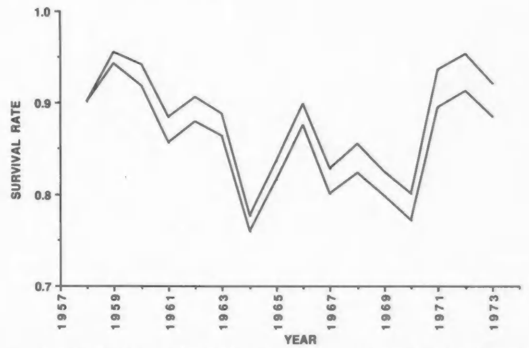

FIG. 6. Comparison of adult female survival rates estimated from age data by weighting with estimates of population size from two versions of the population model. Upper curve shows rates based on weights from model with diminishing reproductive rate; lower curve based on weights from model based on diminishing survival.

A version of the model with reproductive rates declining at a constant rate after 1958 (step 6 of Fig. 1) was used to study diminishing reproductive rates. From 1951 to 1957 the parameter a in equation (2) was maintained at 0.454. Starting in 1958, it was decreased each year by subtracting a quantity, Δ, which was varied in successive simulations in the search for a minimum chi-square. Parameters giving a minimum chi-square in this case yield results that correspond to pup production estimates both for the period for which age structure data are available (1958–74) but also appear to follow the more recent pup population data (York and Kozloff 1987) reasonably well (Fig. 4). Note, however, that the observed values for 1968–70 are well below the projected curve, and the 1975 and 1979 observed pup populations are markedly above the model values.

As an alternative approach, adult female survival rather than reproduction was decreased at a constant rate after 1957 in step 6 of Fig. 1, proceeding in the same manner as for diminished reproduction. Parameters giving a minimum chi-square again gave a reasonably good fit (Fig. 5) to the observed pup population data before and during the period (1958–74) of the pelagic collections, and produced an appreciably smaller overall chi-square (1020 versus 1130 for the diminished reproduction model). A projection of the population trend to recent years is well below the observed data (Fig. 5).

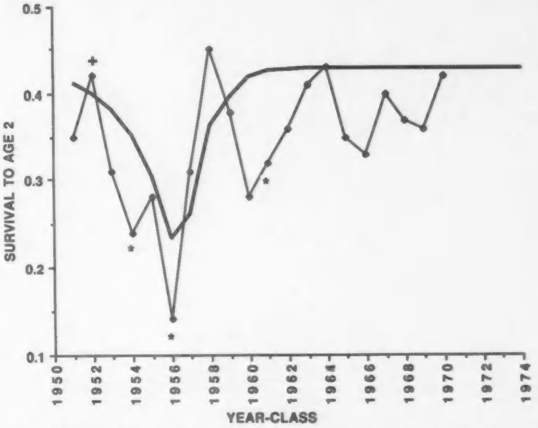

FIG. 7. Survival to age 2 from the diminishing reproductive rate model (solid line) compared with estimates (points) of Lander (1975). Points marked with + or * showed distinct deviations in female age structure persisting over several years when age samples in successive years are compared.

The age structure data supply a possible explanation for this discrepancy. Since the population was changing rather sharply during the period of the pelagic collections, the usual methods of estimating survival from age data will not be suitable. An alternative is to use the model estimates of population size as weights. Annual survival estimates for adult females were obtained as the ratio of proportions aged 5–16 in a given year to the proportion aged 4–15 in the previous year, with each proportion weighted by the population size of the appropriate age group derived from the model. The calculation is:

$$S=\frac{\begin{array}{c}\text{(obsd. prop. 5–16 in year } t\text{)} \times \\ \text{(pop. aged 4–16 in model in year } t\text{)}\end{array}}{\begin{array}{c}\text{(obsd. prop. 4–16 in year } t-1\text{)} \times \\ \text{(pop. aged 4–16 in model in } t-1\text{)}\end{array}}.$$

Since both models fit the observed pup population data reasonably well up to 1974, an initial step in assessing survival from age data is to compare survival estimates obtained by weighting the observed age data by the two models (Fig. 6). Both sources of weights yield a distinct decrease in adult female survival rates through 1970, followed by a recovery for the last 3 yr of the pelagic collections. Such an increase in adult female survival appears to account for the failure of the diminished survival model to fit pup populations in recent years (Fig. 5).

Early survival estimates from the model can be compared (Fig. 7) with rates estimated by Lander (1979; table 2). Due to the density dependence function used, the model results yield a constant survival rate as soon as the population declines well below the maximal population level of about 1956. In the age structure data, several of the year classes show deviations from modelled values that persist over a number of years. The year class of 1952 (denoted by a plus sign in Fig. 7) is consistently larger than adjacent age groups, while those for 1954, 1956, and 1961 (marked by an asterisk in Fig. 7) are distinctly lower than adjacent classes, suggesting that the deviations of Lander's estimates for those years from modelled values very likely rep-

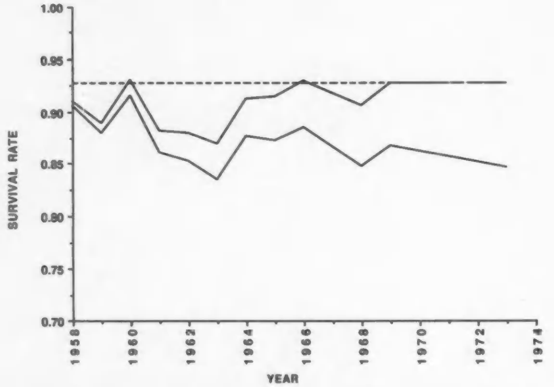

FIG. 8. Comparison of adult female survival rates estimated from two models (upper curve represents diminishing reproductive rate model). Rates were calculated in the same manner as those from age data, i.e. as the ratio of females aged 5 to 16 in one year to those aged 4 to 15 in the previous year. Area between upper curve and dashed line shows approximate impact of harvesting of females on survival rates as calculated from diminishing reproduction model.

resent actual substantial changes in early survival rates for those years.

Discussion

The major objective of the present study has been to assess the female age structure data as a source of information about the failure of the Pribilof fur seal herd to recover after female harvests ceased in 1968. As might be expected, either diminishing reproduction (Fig. 4) or diminishing survival (Fig. 5) provides a realistic-seeming model for the observed trend in pup populations. However, the available data (Fig. 3) on pregnancy rates yields ambiguous evidence as to reality of a decrease in pregnancy rate.

Adult female survival rates estimated from age structure data (Fig. 6) suggest some rather dramatic fluctuations, which appear to be supported by trends in pup populations. An increase in survival in 1965 and 1966 (Fig. 6) was accompanied by a short-term recovery in pup populations (Fig. 5), and the dramatic increase in survival from 1971 to 1973 is also associated with a resurgence in pup population numbers. The situation is complicated by the on-going female harvests, but a useful impression of the likely impact of the harvests can be obtained by contrasting adult female survival rates from the two models (Fig. 8). Without a harvest of females, the upper curve would have remained constant at the rate shown at the right side (there were no female harvests after 1968). Thus it is evident that the main impact of female harvesting occurred in 1961 through 1963, so that harvesting had relatively little direct role in the pattern of survival described above. Note that the survival rates in Fig. 8 are those imposed by structure of the model, i.e. a constant nonharvest survival rate in the upper curve and a continuously declining nonharvest survival rate in the lower curve. Figure 6 gives adult female survival rates estimated directly from the age structure data, with the models serving only to provide weights to adjust for changes in population size from one year to the next.

Since a change of only a few percentage points in adult female survival can have a substantial influence on dynamics of seal populations (Eberhardt and Siniff 1977), it seems clear that the fluctuations evident in Fig. 6 should have dramatic effects on population size, as evidenced in Fig. 5. Further, these results provide a pattern that may be quite useful in seeking an explanation for the observed changes. If one cause of the observed decline in Pribilof fur seal numbers is associated with some specific kind of variable factor, that factor should have been very evident in 1964, diminished in 1966, strongly evident in 1967 through 1970, and virtually ineffective in 1971 through 1973. Inasmuch as either continuously declining reproduction or survival is needed to produce a model trajectory that agrees with observed pup population trends, it seems quite possible that two different factors may be involved in the overall pattern of population change.

Validity of the postulated pattern needs to be assessed through a more intensive study of the data than has been possible with the time and other resources available for the present study. Some sort of confidence bands are needed for the survival rates estimated from the age structure data, since smaller samples of ages are available in some years (cf. York and Hartley 1981; table 2). Since the model plays an essential role in estimating survival, an essential initial step is to attempt to strengthen the model through other data sources.

A major source of additional information not used in the present study is that on male fur seals. Harvest data and counts of bachelor and harem bulls are available over a long time span and need to be exploited in conjunction with the present model, which considers only female fur seals. Lander's (1979) estimates of early survival (Fig. 7) are actually mid-points of two "bounds" on survival, one based on the assumption that all bachelor bulls are harvested, and the other based on an assumed constant escapement rate (Lander 1975). Thus they need further evaluation relative to the density-dependent functions studied in the modelling, and the assumption of the present study that early survival has been constant except for the density-dependent change. As discussed in association with Fig. 7 above, the age data indicate that some age classes show evidence that this assumption is not correct. Also, many of the possible factors influencing adult survival should also affect early survival.

In assessing the results obtained thus far, it should be appreciated that the pup population data has not been used in model fitting, beyond the restriction that parameters giving a minimum chi-square yield a model that passes in the neighborhood of a subset of five pup population estimates (solid points in Figs. 4 and 5). Since the model does seem to match the pup population estimates fairly well, there is independent support for the notion that the age structure data do supply valuable information about the past population dynamics of the herd. One scenario for further study is thus to introduce the adult survival estimates of Fig. 6 into the model, and to attempt further adjustments based on fit of the revised model to pup population estimates. Such a revised model will then supply estimates of bachelor bull abundance for comparison with observed counts (after adjustment for the harvests), and further study of Lander's (1975) method of assessing early survival. Subsequent to submission and review of the present paper, two papers have been published relevant to the material covered here. Trites (1989) evaluated estimation of juvenile survival, and Trites and Larkin (1989) presented two additional simulation models.

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Contribution of *Rhizosolenia eriensis* and *Cyclotella* spp. to the Deep Chlorophyll Maximum of Sproat Lake, British Columbia, Canada

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Experimental fertilization of Sproat Lake with nitrogen and phosphorus greatly increased the abundance of two centric diatoms: *Cyclotella* spp. and *Rhizosolenia eriensis*. A decrease in sinking rates to neutral buoyancy at 17.5–22.5 m, an area of high nutrients and low light, coupled with sedimentation estimates of 10^6–10^7 cells·m^{-2}·d^{-1}, provide strong evidence that diatoms contribute to the formation of a seasonal deep chlorophyll maximum (DCM). The position of the Sproat Lake DCM, occurring at or just above the 1% light depth, appears to be largely determined by the light regime. *R. eriensis* bloomed and sank out of the mixed layer early in the spring before lake fertilization began. Immediately after fertilization, concentrations of nitrate and phosphate were elevated for 1 h only in the top 1 m of the water column. Most *R. eriensis* cells were well below 1 m and benefited little from the nutrient addition because of temporal and spatial separation. *Cyclotella* spp. occurred in the upper epilimnion and bloomed later in the year and consequently benefited (by large density increases) from fertilization. It is important to consider the temporal and spatial distribution of phytoplankton in determining which species will increase in abundance as a result of areal fertilization.

L'apport expérimental d'azote et de phosphore dans le lac Sproat a mené à une forte augmentation de l'abondance de deux diatomées centriques, soit *Cyclotella* sp. et *Rhizosolenia eriensis*. Une baisse des taux de descente en profondeur à un taux de flotabilité neutre à une profondeur allant de 17,5 à 22,5 m, une zone de concentration élevée de bioéléments et de faible lumière, en plus de taux de sédimentation estimatifs allant de 10^6 à 10^7 cellules·m^{-2}·d^{-1}, sont de solides preuves que les diatomées contribuent à la présence d'un maximum saisonnier de chlorophylle en profondeur (DCM). La position du DCM dans le lac Sproat, situé à la profondeur où l'intensité lumineuse se situe à 1 % ou juste au dessus, semble en grande partie fixée par le régime lumineux. La prolifération de *R. eriensis* et sa disparition de la zone mélangée a eu lieu au début du printemps avant la fertilisation lacustre. Immédiatement après celle-ci, seul le premier mètre de la colonne d'eau a montré des concentrations élevées de nitrate et de phosphate et ce, pendant 1 h seulement. La plupart des cellules de *R. eriensis* étaient concentrées bien au-dessous du niveau de 1 m et ont peu bénéficié de l'apport de bioéléments à cause de la séparation temporelle et spatiale. *Cyclotella* sp. était présente dans la partie supérieure de l'épilimnion et, comme elle a proliféré plus tard, elle a bénéficié de la fertilisation. Il est donc important de tenir compte de la répartition temporelle et spatiale du phytoplankton dans la détermination des espèces qui prolifèreront après une fertilisation de surface.

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The joint Canadian Federal–Provincial Salmonid Enhancement Program has as one of its goals the enhancement of declining sockeye salmon (*Oncorhynchus nerka*) stocks. Fertilization of selected oligotrophic lakes with inorganic nitrogen and phosphorus has increased primary and secondary production and has resulted in the availability of more food for juvenile sockeye salmon (Barraclough and Robinson 1972; Stockner 1981, 1987). However, an increase in primary production may not always lead to a successful lake enrichment program because the phytoplankton species that are enhanced may not be grazed by zooplankton (e.g. due to cell size or chemosensory inhibition). Therefore, it would be desirable to enhance only the grazeable phytoplankton species possibly by altering nutrient ratios or frequency of addition of the added nutrients (Turpin and Harrison 1979; Harrison and Turpin 1982).

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A common and abundant pelagic diatom, *Rhizosolenia eriensis*, has increased in some lakes following nutrient enrichment (Parsons et al. 1967; Stockner et al. 1980). Following spring increases this diatom sinks and becomes a major constituent of a deep chlorophyll maximum (DCM) in some lakes (Stockner and Hyatt 1984). Incorporation of *R. eriensis* into the DCM typically occurs near the compensation depth concurrent with the nitracline (Jackson 1988). This species is characteristically large and elongate with spines (100–150 μm) and herbivorous zooplankton may not be capable of grazing it efficiently (Parsons et al. 1967). Consequently, enhancement of this species by nutrient enrichment of a lake and subsequent incorporation into the chlorophyll maximum may represent an energy loss or carbon sink, diverting added nutrients from major food chains leading to juvenile sockeye production (Shortreed and Stockner 1989).

The main objectives of this study were (1) to determine the contribution(s) of *R. eriensis* and *Cyclotella* spp. to the DCM, (2) to establish whether low light and high nutrient concentrations act together to reduce the sinking rate of both diatoms so they become neutrally buoyant and form a layer at a specific depth, and, (3) to determine if the added nutrients were enhancing *R. eriensis* and *Cyclotella* spp. or being used by other phytoplankters.

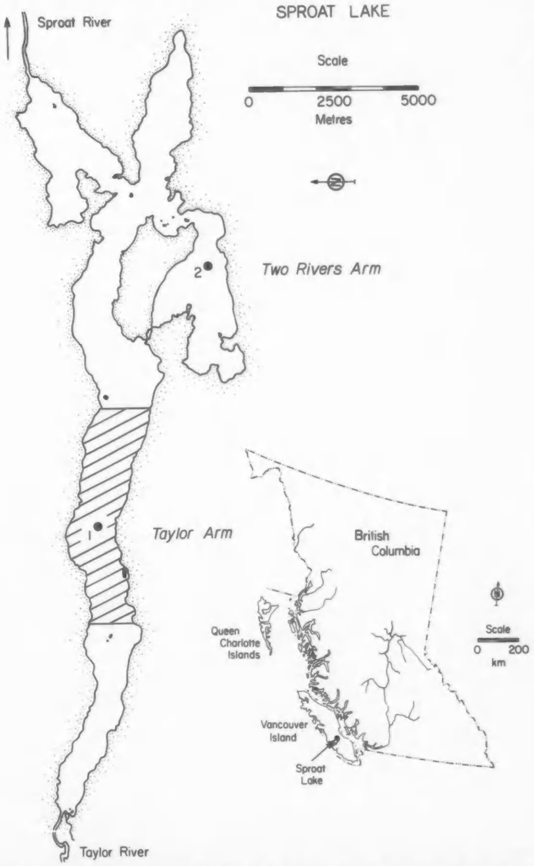

FIG. 1. Location and map of Sproat Lake, British Columbia, Canada. Fertilized (1) and unfertilized (2) stations are indicated. The hatched area of Taylor arm received nutrient enrichment.

Materials and Methods

Sproat Lake (49°14′N, 125°06′W) is located on central Vancouver Island, British Columbia (Fig. 1). The lake is approximately 22.5 km long, 1.5 km wide with a surface area of 41 km^2, mean depth of 56 m, maximum depth of 270 m and an elevation of 26 m above sea level. The littoral zone is greatly reduced with shorelines sloping abruptly into deep water. Sproat Lake is a warm monomictic coastal lake with low inorganic nutrient levels, low phytoplankton and zooplankton biomass and a water residence time of about 8 yr (Stockner and Shortreed 1985).

Two stations were sampled: Station 1 in Taylor Arm which received areal nutrient enrichment in 1986 from May to July but not in 1987, and Station 2, the control station in Two Rivers Arm which received no nutrient enrichment (Fig. 1). Data were collected over 2 yr from 1 April to 9 August in 1986 and from 7 March to 1 June in 1987.

Samples for nutrients and phytoplankton were obtained from bottle casts at five or six discrete depths in the upper 30 m, while samples for temperature were obtained from up to 17 discrete depths using a reversing thermometer attached to a van Dorn water bottle. Light intensity was measured with a Li-Cor quantum light meter (model 185A) equipped with an underwater cosine collector (model 192S). Measurements were made just below the surface and at metre intervals to approximately 20 m. Nutrient samples were placed in acid-washed 1-L polyethylene bottles for transport to the laboratory. Water samples were filtered in the lab through precombusted and prewashed 47-mm glass fibre filters (Whatman GF/F) and stored in acid-washed glass bottles with foil-lined screwtop caps at 2°C for 8 to 20 wk. Nitrate was analysed by a modified version of the seawater technique of Brewer and Riley (1975) with a detection limit of 1 $\mu g\ NO_3-N \cdot L^{-1}$. Total phosphorus (TP) and total dissolved phosphorus (TDP) were analysed by a modification of the method of Traversy (1971) with a detection limit of 1 $\mu g\ P \cdot L^{-1}$.

Before thermal stratification occurred, temperature was measured at 0.5 m and then every 5 m from 5 to 50 m; after stratification it was measured at 0.5 m, every 2.5 m from 2.5 to 27.5 m, then every 5 m from 30 to 50 m.

In vivo fluorescence was measured with a Turner Designs fluorometer (model 10) equipped with filters to measure chlorophyll *a* and modified for flow-through operation. A diaphragm pump (Jabsco electric bilge pump, model 34600-0000) was run for a minimum of 60 s prior to taking a reading to ensure flushing the hose of the previous sample. Depths sampled were 0.5 m then every 2.5 m from 2.5 to 27.5 m and every 5 m from 30 to 50 m. The time between successive sample dates varied from 3 to 5 d. Depths sampled for phytoplankton depended on the vertical distribution of chlorophyll, as estimated by the fluorescence profile on each sampling date. Plastic 1-L bottles were filled from water bottle casts, and upon return to the laboratory, subsamples were taken for immediate enumeration and for long term storage. These samples were fixed and preserved with Lugol's iodine solution containing acetic acid (Sournia 1978). Phytoplankton identification and enumeration (a minimum of 200 cells were counted giving

±5% counting error) was by the Utermohl technique (Utermohl 1958) using a Wild M40 inverted microscope equipped with phase contrast optics at either 200 or 600 × magnification. The following species or groups were enumerated: *Rhizosolenia eriensis*, *Cyclotella* spp. the dominant *Cyclotella's* in Sproat Lake are: *C. kutzingiana*, *C. stelligera*, *C. ocellata*, and *C. comta* (Stockner and Costella 1980)), *Asterionella formosa*, *Fragilaria* sp., *Synedra* sp., *Melosira* sp., *Dinobryon* sp., ciliates, cysts, small (3–15 μm) and large (>15 μm) flagellates and others. Details are given in Jackson (1988).

A SETCOL apparatus (Bienfang 1981) was used to estimate duplicate sinking rates of the phytoplankton sampled from 5, 10, 17.5, and 22.5 m on 9 and 20 May, 1987. A cooling water bath and water jackets around the SETCOL tubes ensured that temperature was constant during the experiments. Natural light was used and the intensity was varied by using cheesecloth screening. Temperature and light conditions used during the sinking rate experiments were chosen to approximate values found at depths from where water samples were obtained. The experiments were run for 4 h and the cell density of the species present in the natural assemblage was used as the measure of biomass for sinking rate calculations (Bienfang 1981).

Paired sediment traps were 51 cm high and 12.5 cm in diameter with a baffle in the mouth of the trap (complete details are given by Sancella and Calvert 1988). They were deployed at 15 m at both stations. A 1.5% NaCl solution (to kill grazers and maintain a high density solution) was placed in the collection cup. Phytoplankton were collected (after 7-d exposure periods during 1986, 4-d exposure periods during 1987), preserved and enumerated as previously described for phytoplankton.

During 1985 and 1986 Taylor Arm was fertilized weekly by air using a DC6B water bomber while Two Rivers Arm was not fertilized. The phosphorus loading rate was 2.5 mg $P{\cdot}m^{-2}{\cdot}wk^{-1}$ for 18 wk at an atomic N:P ratio of 25:1. Neither arm was fertilized during 1987. Procedures of lake fertilization have been previously described (Stockner et al. 1980; Stockner and Shortreed 1985; Stockner 1987).

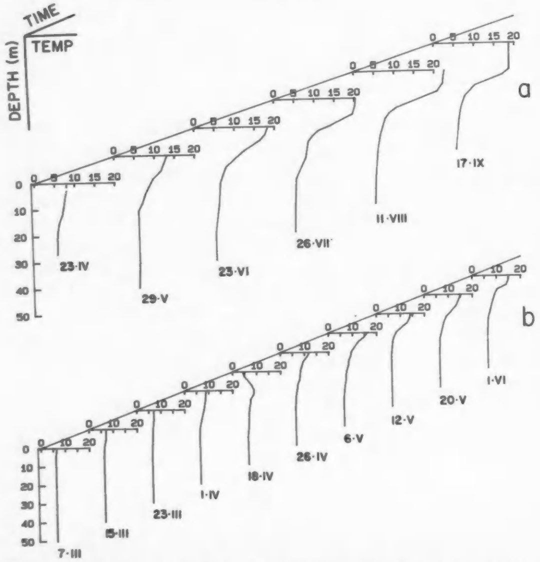

FIG. 2. Temperature profiles of Taylor arm during 1986 (a) and 1987 (b).

Results

Temperature

In April 1986 the lake had begun to stratify (Fig. 2a). The surface temperature was approximately 8°C and throughout the sampling period stratification intensified. The maximum surface temperature was 23.1°C on 11 August. From the temperature profiles, the epilimnion was estimated to be 0–10 m, the metalimnion 10–17.5 m and the hypolimnion 17.5–bottom.

The first profile on 7 March 1987 (Fig. 2b) showed isothermal conditions from 0–50 m. By 1 April thermal stratification had commenced and intensified through early June, when surface temperatures reached 15°C. In general, the temperature profiles of both arms were similar. Depths of the epilimnion, metalimnion, and hypolimnion were 0–7.5 m, 7.5–12.5 m, and 12.5–bottom, respectively.

Light

The depth of 1% surface irradiance was generally deeper in the control arm than in the experimental arm (except for late summer, 1986) during both years (Jackson 1988). The control arm compensation depth varied from 15.5–22 m while values for the experimental arm ranged from 15–20 m.

Nitrate

In the control arm during 1986, epilimnetic nitrate was below detection limits after 28 May (Fig. 3a). The nitracline began at 15 m and increased to 40 m, the lowest depth sampled, where it ranged from 30–40 $\mu g\ N{\cdot}L^{-1}$. In the fertilized arm, although at low concentrations, nitrate was detectable in the epilimnion until sometime between 25 June and 23 July.

Total Phosphorus (TP) and Total Dissolved Phosphorus (TDP)

The maximum TP measured in the control arm during 1986 and 1987 was 6 $\mu g\ P{\cdot}L^{-1}$ while in the experimental arm it was 4 and 3 $\mu g\ P{\cdot}L^{-1}$ in 1986 and 1987, respectively. Throughout most of the sampling periods however, TP and TDP were generally <2 $\mu g\ P{\cdot}L^{-1}$.

In vivo Fluorescence

On 27 May 1986 a fluorescence maximum (FM) was already present at both stations (Fig. 4a). The FM increased in the control arm until mid-June, when it reached a chlorophyll equivalent value of 2.4 $\mu g\ Chl\mathit{a}{\cdot}L^{-1}$ at 22.5 m (58% of areal chlorophyll, i.e. chlorophyll per square metre, was within the chlorophyll maximum). In the experimental arm the FM formed more slowly and attained a maximum of 2.6 $\mu g\ Chl\mathit{a}{\cdot}L^{-1}$ at a depth of 22 m, with 55% of areal chlorophyll within the chlorophyll maximum. On 3 July, in addition to the seasonal FM at 22.5 m there was a second peak at 10 m which coincided with an epilimnetic bloom of algal picoplankton (Shortreed and Stockner 1989). These two peaks contained 24 and 47% of areal chlorophyll in the 10 m and 22.5 m peaks, respectively.

A FM (2.2 $\mu g\ Chl\mathit{a}{\cdot}L^{-1}$) formed at 12.5–15 m (66% of areal chlorophyll) in the control arm by mid-April 1987 and descended to 20 m by 1 June (Fig. 4b). In the experimental arm similar profiles occurred approximately 2 wk later.

Phytoplankton

Rhizosolenia eriensis and *Cyclotella* spp. were the two dominant phytoplankters in Sproat Lake during 1986 and 1987 and

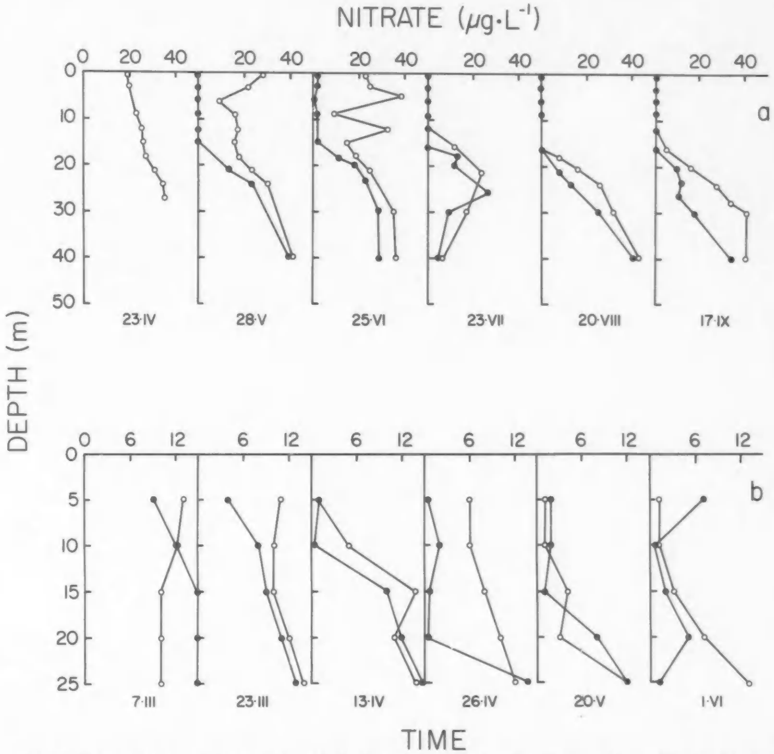

FIG. 3. Nitrate concentration during 1986 (a) and 1987 (b) in Two Rivers (●) and Taylor (○) arms.

therefore the focus of this paper in terms of species composition. Other species are discussed in more detail in Jackson (1988). *Rhizosolenia eriensis* bloomed prior to lake enrichment and prior to *Cyclotella* spp. in the spring. Throughout the spring and summer, small flagellates and on occasion, *Dinobryon* sp. were important numerically (Jackson 1988). Later in the summer, other diatoms (*Asterionella formosa, Synedra* sp., and *Flagilaria* sp.) became more important numerically but were not as important as *R. eriensis* and *Cyclotella* spp.

The low concentrations of *R. eriensis* present at the beginning of the 1986 field season (May) were almost absent from 0–30 m by the end of July in both arms (Fig. 5a). In mid-May 1986, *Cyclotella* spp. were rare in both arms with low cell densities until late June when there was an increase to 72 cells·mL^{-1} at 5 m in the fertilized arm (Fig. 6a).

By mid-April 1987, there was a pronounced peak in abundance of *R. eriensis* at 10 m (260 cells·mL^{-1}) and on 28 May a much larger peak was observed at 15 m (6100 cells·mL^{-1}) in the control arm. However, *R. eriensis* cell density throughout the water column in the experimental arm was usually below 50 cells·mL^{-1} during this period.

Sedimentation

The cell flux of *R. eriensis* was low (10^6 cells·m^{-2}·d^{-1}) during early spring (1987), high (10^7 cells·m^{-2}·d^{-1}) during the spring/summer transition and low (10^6 cells·m^{-2}·d^{-1}) during the summer (Fig. 7). During the 1986 period of fertilization, cell flux was usually greater in the experimental arm. Throughout the summer of 1986, *R. eriensis* cell flux decreased in contrast to *Cyclotella* spp. which increased and was greater in the fertilized arm near the end of the sampling period. The total cell flux of both diatoms was much lower in 1987 than in 1986.

Sinking Rate Determination

The sinking rate of *R. eriensis* was similar for 9 and 20 May at both sites at 5 and 10 m, ranging from 1.8–2.2 m·d^{-1} (Fig. 8). The lowest sinking rates occurred at 22.5 m. *Rhizosolenia eriensis* sank significantly faster ($p<0.05$) at 17.5 m on 9 May than on 20 May. Similar results were obtained with *Cyclotella* spp. with the lowest sinking rates occurring at 22.5 m.

Discussion

Vertical fluorescence profiles clearly document the sequence of the spring bloom in Sproat Lake. Phytoplankton growth was initiated sometime in mid-March and there was an accompanying increase in fluorescence in the surface waters down to 10–12 m. At this time water temperatures increased, stratification began and the extinction coefficient increased, signalling the beginning of the spring phytoplankton increase. A subsurface FM formed quickly in late March and was well established at 15 m by mid-April. This maximum may have resulted from increases in chlorophyll, an increase in fluorescence per unit chlorophyll, and/or from in situ cell growth and or sinking to 15 m.

As the mid-March peak was found above the 1% light depth, a positive net rate of photosynthesis and growth was maintained during the early spring period in Sproat Lake. Light was shown

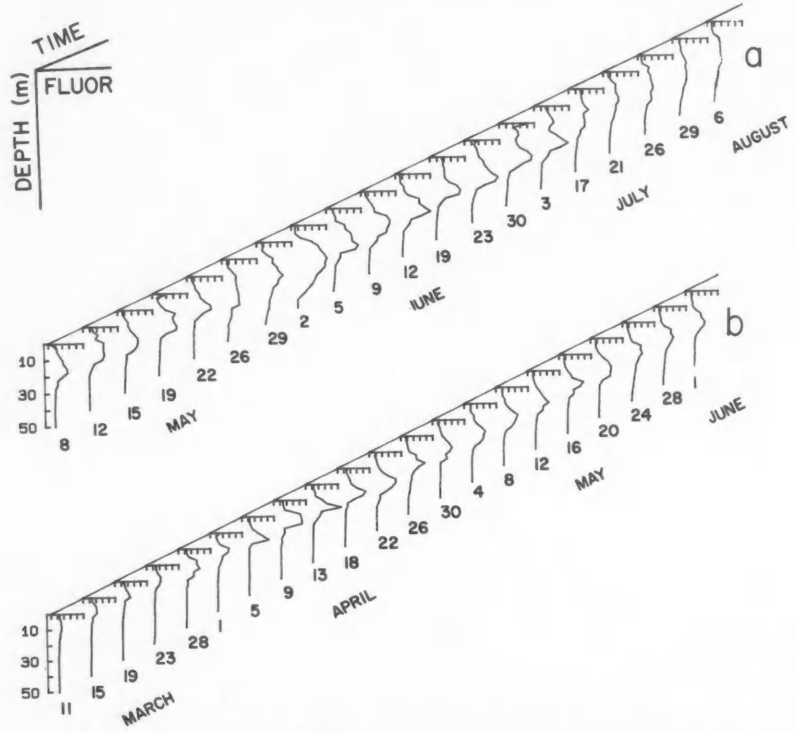

FIG. 4. In vivo fluorescence profiles of Taylor arm during 1986 (a) and 1987 (b).

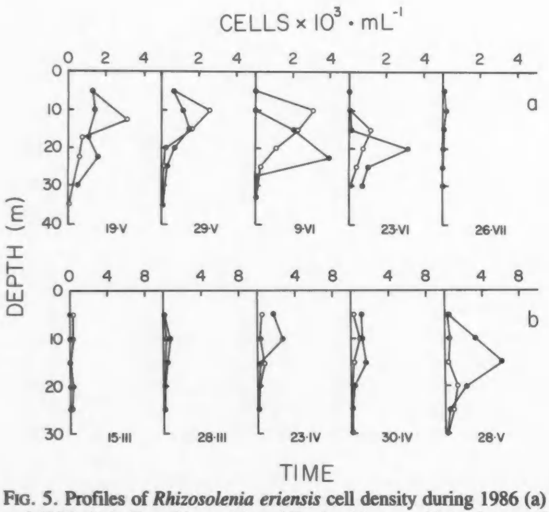

FIG. 5. Profiles of *Rhizosolenia eriensis* cell density during 1986 (a) and 1987 (b) in Two Rivers (●) and Taylor (○) arms. Note change of scale in (b).

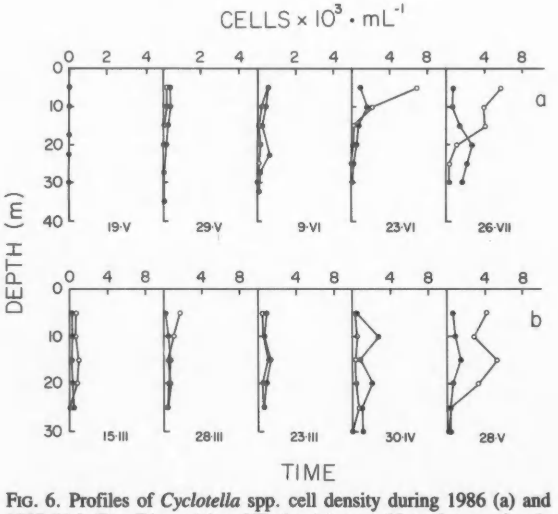

FIG. 6. Profiles of *Cyclotella* spp. cell density during 1986 (a) and 1987 (b) in Two Rivers (●) and Taylor (○) arms. Note change of scale in (b).

to be important in determining the vertical position of the DCM in Lake Michigan also, where Moll et al. (1984) demonstrated that phytoplankton within the DCM could grow in low light and contributed up to 60% to areal primary production.

By May, nutrient concentrations had declined abruptly while the extinction coefficient, fluorescence, *R. eriensis* abundance and thermal stratification were increasing. *R. eriensis* and *Cyclotella* spp. sank slower under conditions of low light and high nutrients than they did under conditions of high light and low nutrients. This decrease in sinking rate at depth when these two diatoms encountered lower light and higher nutrients could

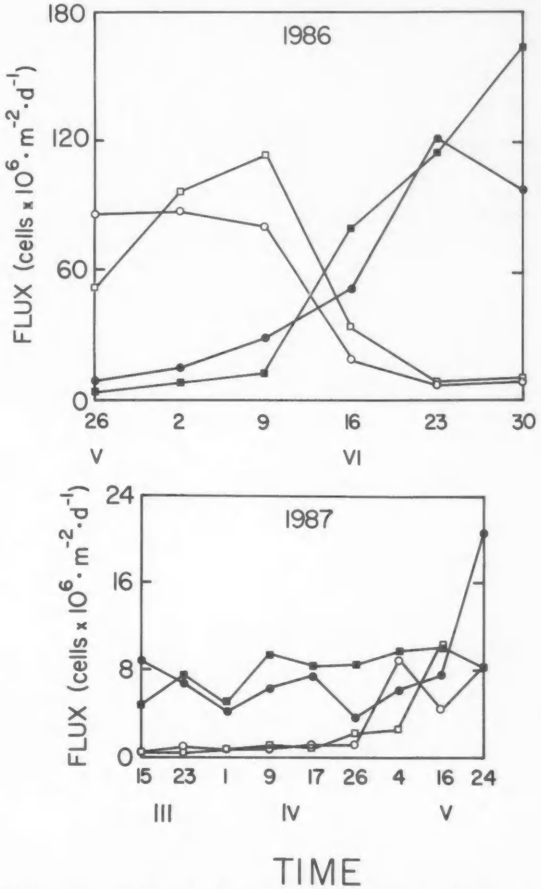

FIG. 7. Sedimentation rate at 15 m of *Rhizosolenia eriensis* (open symbols) and *Cyclotella* spp. (closed symbols) in Two Rivers (● and ○) and Taylor arm (■ and □).

well have been a major factor leading to the formation of the DCM.

The sediment trap and sinking rate results together provide strong supporting evidence that diatoms are a major contributor to the DCM. Our cell flux data suggest that a large number of these diatoms (10^6–10^7 cells·m^{-2}·d^{-1}) sink through the epilimnion, and our sinking rate data show that they achieve near neutral buoyancy in the DCM under conditions of low light and higher nutrients.

The summer period was characterised by (1) strong, stable stratification, (2) extremely low nutrient concentrations in the epilimnion, (3) a nitracline at 15 m, and (4) a well developed FM at 22.5 m. Chlorophyll, *R. eriensis*, and small flagellates were maximal at 20 m (Jackson 1988), with a large portion of the phytoplankton biomass located in the DCM.

By late June, *Cyclotella* spp. displaced *R. eriensis* as the dominant diatom in the epilimnion and responded more favourably to nutrient enrichment than other species given the considerably higher increase in cell density during late June and July in the fertilized arm.

In the absence of measurable dissolved phosphorous and nitrogen in the epilimnion, phytoplankton growth may have occurred at low rates, possibly utilizing recycled phosphorus and nitrogen (Lehman 1980; Stockner and Shortreed 1985). At the DCM there was measurable nitrate and cells were probably P-limited since phosphorus was below the detection limit. Below the 1% light depth, autotrophic growth was clearly light-limited. Most of the DCM existed in the hypolimnion within the nitracline and above the 1% light depth. At such depths, phosphorus would likely by supplied by bacterioplankton (microbial loop), zooplankton excretion and sloppy feeding (Lehman 1980; Williams 1981).

In late June 1986, the abrupt disappearance of the DCM following cessation of fertilization in the experimental arm resulted from a large picoplankton increase (Shortreed and Stockner 1989), which caused a marked decrease in transparency (Secchi depth 5.5 m in the fertilized arm versus 11.0 m in the control arm). Battoe (1985) also noted a decline of the DCM in a subtropical lake resulting from decreased light penetration due to increased epilimnetic algal production and inorganic turbidity.

Cyclotella spp. also increased in abundance in the epilimnion at this time likely as a result of fertilization because no increase occurred in the control arm. By late August, after the disappearance of the 10-m maximum, transparency increased and the FM was again reestablished at 25 m. This event points to the possible importance of light in the formation, maintenance and positioning of the DCM. During July and August, nutrients were similar at depths of the DCM and therefore it appears that the DCM was affected more by light than nutrients.

The ability of *R. eriensis* to grow rapidly in the early spring and maintain itself in the region of the DCM throughout the summer indicates this diatom is well adapted to lower temperatures (5–15°C) and, since it was one of the first species to bloom in the spring, it may also have a lower light requirement than other species. In late spring it sinks out of the epilimnion, achieving neutral buoyancy and becoming a major constituent of the DCM. It is therefore unlikely that *R. eriensis* was a large nutrient loss during the lake fertilization experiment because it was present in substantial numbers in the epilimnion only during the early portion (March–May) of the spring bloom, prior to the first treatment (late-May).

Lake Fertilization and its Effect on *R. eriensis*

A critical factor linking *R. eriensis* population enhancement to lake fertilization might be the timing of the commencement of fertilization in relation to the status of *R. eriensis* population dynamics. If *R. eriensis* is growing and present in sufficient numbers in the epilimnion, fertilization might benefit the population, as was the case for *Cyclotella* spp. However, if the population has declined and sunk out of the epilimnion, and is in poor physiological state as was the case for Sproat Lake during 1986, fertilization might not have a noticeable effect. If the beginning of fertilization overlaps the period of optimal growth of *R. eriensis* in the spring then this species may be enhanced. In this case, *R. eriensis* would be a nutrient and carbon sink if it was not grazed. Previous studies have demonstrated that phytoplankton community composition can be altered by the frequency of limiting addition (Turpin and Harrison 1979; Suttle et al. 1987; Suttle et al. 1988; Suttle and Harrison 1988) and nutrient ratios (Titman 1976; Tilman 1977, 1981; Suttle and Harrison 1988).

Measurements of nitrate and phosphate immediately after fertilization (Stockner 1987) revealed that concentrations of these two nutrients were only elevated in the top metre of the

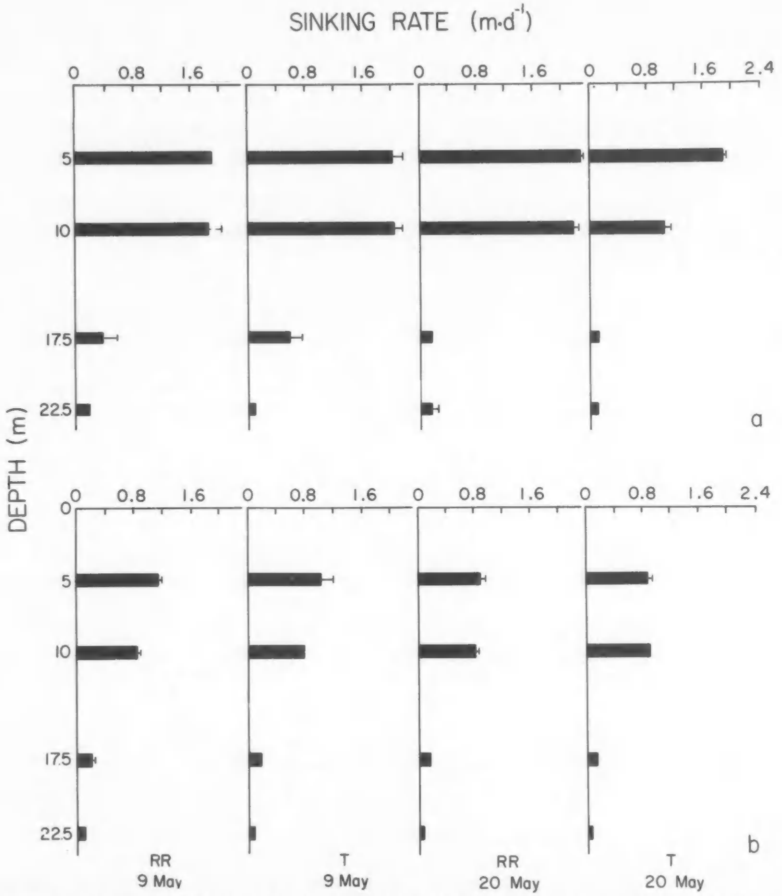

FIG. 8. Sinking rates of *Rhizosolenia eriensis* (a) and *Cyclotella* spp. (b) on 9 and 20 May 1987 in Two Rivers (RR) and Taylor (T) arms. Error bars represent ±2 SD.

water column. Therefore, cells of *R. eriensis* in the lower portion of the epilimnion or at the DCM would not benefit from lake enrichment practices. This example points out the importance of considering both the temporal and spatial distribution of a species in determining which phytoplankton species are enhanced by nutrient enrichment of a lake.

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Recycling of Elements Transported Upstream by Runs of Pacific Salmon: I. δ^{15}N and δ^{13}C Evidence in Sashin Creek, Southeastern Alaska[1]

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Kline, T. C. Jr., J. J. Goering, O.A. Mathisen, P. H. Poe, P. L. Parker. 1990. Recycling of elements transported upstream by runs of Pacific Salmon: I. δ^{15}N and δ^{13}C evidence in Sashin Creek, southeastern Alaska. Can. J. Fish. Aquat. Sci. 47: 136–144.

Values of δ^{15}N and δ^{13}C (the per mil deviation from the recognized isotope standard) from biota of a southeastern Alaska stream (Sashin Creek) that receives an annual run of 30 000 anadromous pink salmon (*Oncorhynchus gorbuscha*) were measured to determine sources of nitrogen (N) and carbon (C). Marine-derived nitrogen (MDN) is the predominant source of N for food webs found in the lower 1200 m of the stream which, due to a waterfall, is the only portion of the stream available to salmon returning to spawn. Comparable spawning section biota were enriched by about 5 per mil relative to the salmon-free control section, corresponding to the difference between 0 and 100% MDN in a mixing model. Food webs of resident rainbow trout (*O. mykiss*), at the outlet of one of the source lakes, Sashin Lake, have very low δ^{13}C, suggesting the importance of a respired C pool in the lake. The source of C in the remainder of the stream is C fixation by autochthonous producers and marine organic C (within the salmon spawning section). Resident fishes in the salmon spawning section depend on MDN and some of the C delivered by the annual run of returning salmon.

On a quantifié les concentrations de δN^{15} et de δC^{13} (la déviation par millième par rapport à l'isotope étalon reconnu) chez la biote d'un cours d'eau du sud-est de l'Alaska (ruisseau Sashin) fréquenté par une remontée annuelle de 30 000 saumons roses (*Oncorhynchus gorbuscha*) anadromes afin de déterminer l'origine de l'azote (N) et du carbone (C). L'azote d'origine marine (MDN) est la principale source de N des réseaux alimentaires présents dans les premiers 1 200 m du cours d'eau qui, à cause d'une chute, est la seule partie fréquentée par les saumons reproducteurs. La biote analogue peuplant les frayères était enrichie d'environ 5 par millième par rapport au tronçon témoin libre de saumon, ce qui correspond à une différence du MDN allant de 0 à 100 % dans le modèle de brassage. Les réseaux alimentaires de la truite arc-en-ciel (*O. mykiss*) résidente, à l'émissaire d'un des lacs d'origine (lac Sashin) montrent une très faible concentration de δC^{13}. Ceci laisse supposer un important apport de C par respiration dans le lac. Dans l'autre partie du cours d'eau, le carbone provient de la fixation par les producteurs autochtones et d'une source de C organique marin (dans les frayères à saumon). Les poissons résidents peuplant les frayères à saumon dépendent du MDN et d'une partie du C dérivés de la remontée annuelle du saumon.

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Geochemistry has traditionally been concerned with the transport of material by rivers to the sea. The life history of Pacific salmon and the physical geography of southeast Alaska combine to provide an opportunity to detect the reverse, i.e. the transport of nutrients from the ocean to freshwater. Large increases in the abundance of dissolved nutrients occur in streams following the massive die-off of spawned-out Pacific salmon, *Oncorhynchus* spp. (Brickell and Goering 1970; Richey et al. 1975; Sugai and Burrell 1984). Krohkin (1967) and Donaldson (1967) suggested that, based on comparisons of carcass contribution with other inputs and nutrient abundance in high-latitude sockeye salmon (*O. nerka*) lakes, the biogenic input of nutrients can be significant. According to Krohkin (1967), the phosphorus (P) budget of sockeye salmon lakes could be significantly affected by variation in escapement of mature salmon into the spawning system if the salmon P input was only 25% of the total input. It has been argued that dilution of biogenic nutrient loading into a large-volume lake (e.g. Iliamna Lake, Bristol Bay, Alaska: 117 km^3) would reduce the significance of the input (Krohkin 1967; Durbin et al. 1979). Krohkin (1967) suggested a minimum of 500 salmon/10^6 m^3 for biogenic P input to be significant. However, from the case studies of Iliamna Lake, it has been hypothesized that rapid uptake of the biogenic input of nutrients from decomposing salmon carcasses by benthic algae (periphyton) could sequester the nutrients and make them available to freshwater food webs (Donaldson 1967; Mathisen 1972). Direct consumption of salmon eggs and fry may also be significant in supporting higher trophic level organisms, especially rainbow trout (*O. mykiss*, formerly known as *Salmo gairdneri*) and Dolly Varden (*Salvelinus malma*).

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In the RETURNS (Recycling of Elements Transported Upstream by Runs of Salmon) project, natural abundance of nitrogen (N) stable isotopes was used to trace the incorporation of biogenic marine-derived N (MDN) into the food webs of several Alaskan freshwater systems. Identification of MDN by use of measurements of $^{15}N/^{14}N$ at the natural abundance level provided unique evidence that a significant source of the nutrients being utilized by freshwater salmon-producing ecosystems is returning salmon. The use of $\delta^{15}N$ (see definition in Materials and Methods section) in food web investigations dates from the work of DeNiro and Epstein (1981) and Schoeninger et al. (1983). Carbon (C) stable isotope ratios were used to trace the utilization of fixed C in concert with $\delta^{15}N$. The use of $\delta^{13}C$ (see definition in Materials and Methods section) in food web studies has been reviewed by Fry and Sherr (1984).

In the study reported here, variations in the natural abundance of stable C and N isotopes were used to trace the biological utilization of MDN transported by adult spawning salmon into a short (1200 m) coastal stream in southeastern Alaska. The use of stable isotopes is based on the observation that marine N is enriched in ^{15}N relative to terrestrial and freshwater N; therefore, $\delta^{15}N$ values can be used to differentiate between N from marine and freshwater sources (Schoeninger et al. 1983; Minagawa and Wada 1984; Owens 1987). The premise behind this study is that without marine N input the biota isotope ratios would reflect the alternative N source, atmospheric N. Atmospheric N_2, by definition, has a $\delta^{15}N = 0$. Other forms of atmospheric N, such as NH_4^+ and NO_3^- in precipitation, have a $\delta^{15}N$ of -1.4 ± 3.5 and -6.6 ± 3.9, respectively (Hübner 1986). There is little isotopic fractionation of N during N_2 fixation (Hoering and Ford 1960; Delwiche and Steyn 1970); thus, primary production derived from atmospheric N_2 results in biota with $\delta^{15}N$ values near 0 (Minagawa and Wada 1984). Because isotopic fractionation during utilization of fixed N (Wada 1980) is influenced by the proportion of the dissolved inorganic nitrogen (DIN) pool that is depleted (Owens 1987), $\delta^{15}N$ of non-N_2-fixing primary producers is expected to vary relative to the starting $\delta^{15}N$ value of the DIN source. If most of the N pool is utilized the particulate pool $\delta^{15}N$ will equal the source $\delta^{15}N$ value. Otherwise, isotopic discrimination by algae using $^{14}NH_4^+$ and $^{14}NO_3^-$ in preference to $^{15}NH_4^+$ and $^{15}NO_3^-$ will result in primary producers being enriched in ^{14}N relative to the DIN pool (Wada 1980; Owens 1987). $\delta^{15}N$ values obtained for primary producers in salmon-free systems were 0 ± 2 per mil (Kline et al. 1986; Mathisen et al. 1988) and thus strongly supported the contention that recently fixed atmospheric N_2 was the N source.

A $\delta^{15}N$ value of returning salmon of $+11.2 \pm 1.0$ (Mathisen et al. 1988) was used to establish a mixing model (Fig. 1) based on Fry and Sherr (1984). $\delta^{15}N$ values of 0 and +11 were used as the endmembers (source values) representing the two N sources, the atmosphere and salmon, respectively. The model was developed for data interpretation, to relate the observed $\delta^{15}N$ values to percent MDN. Values of 0 and +11 were the absolute endmembers for N in this system because they were the values observed for the two N sources. However, isotopic discrimination by algae, which usually results in isotopic fractionation during utilization of the dissolved N pool (Wada 1980), needed to be incorporated into the mixing model. The fractionation is variable (Wada 1980), with the greatest effect occurring in N-rich waters (e.g. Antarctica, Wada et al. 1984) and the minimal effect in oligotrophic waters where the $\delta^{15}N$ of algae equals that of the source (Minagawa and Wada 1984; Owens 1987). The possible $\delta^{15}N$ range for primary producers using MDN based on these extremes was +5 (maximal fractionation) to +11 (no fractionation). Note that a primary producer value in this range is distinguishable from primary producers deriving their N from N_2 fixation with $\delta^{15}N$ values near 0 (Minagawa and Wada 1984). Empirical primary producer (periphyton) $\delta^{15}N$ values were used to establish a preliminary mixing model (Kline et al. 1986; Mathisen et al. 1988). Data obtained during this study were used to verify the primary producer empirical endmembers of 0 and +7 for 0 and 100% MDN, respectively.

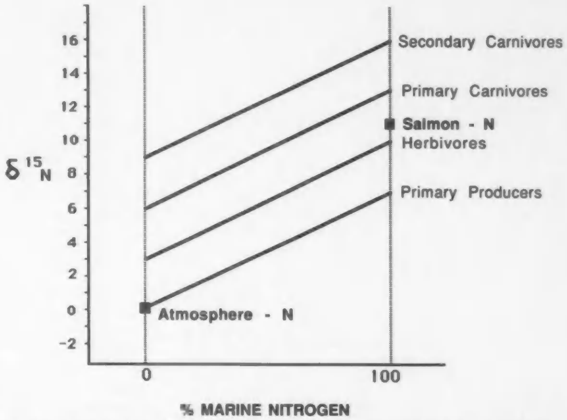

FIG. 1. RETURNS $\delta^{15}N$ mixing model. Principal N sources are shown as black boxes. $\delta^{15}N$ of salmon from Mathisen et al. (1988, and unpubl. data).

The isotopic fractionation by consumers of about +3 (DeNiro and Epstein 1981; Minagawa and Wada 1984; Wada et al. 1987; Parker et al. 1988) was used to extend the mixing model to higher trophic levels (Fig. 1). This made it possible to determine the significance of the two N sources at higher tropic levels.

The approach used in this study was to compare $\delta^{15}N$ of biota from the lower part of a freshwater system with $\delta^{15}N$ of biota from the upper part of the system which is isolated from returning anadromous fishes by a 30-m waterfall. Because the upper stream does not receive the very positive $\delta^{15}N$ marine N of salmon, it serves as a control and allows a test of the hypothesis that MDN dominates the biogeochemistry of the salmon-spawning habitat.

Study Site

Sashin Creek is located at the south end of Baranof Island in southeastern Alaska, USA, near 56°23′N and 134°44′W. The system, 4 km in length, located in coastal coniferous forests adjacent to mountains, receives considerable annual precipitation (5.6 m). Two lakes, Sashin and Round, drain into the stream.

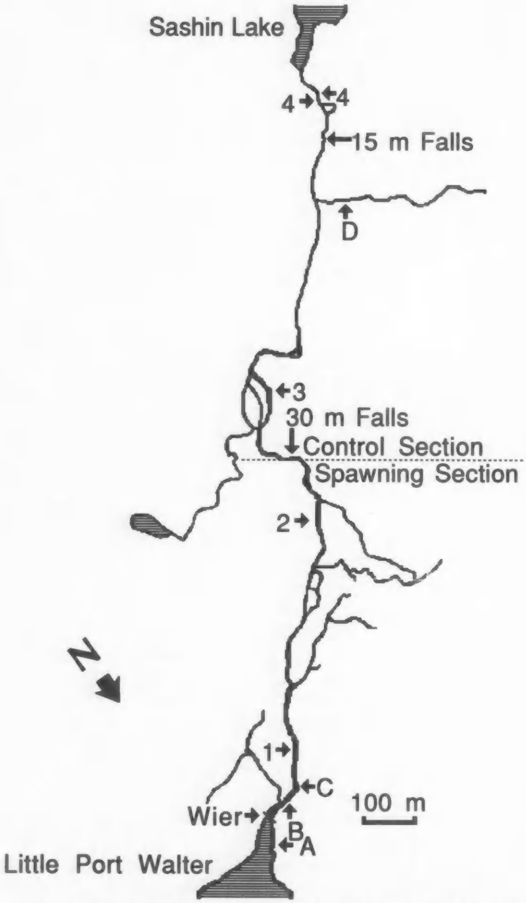

FIG. 2. Sashin Creek from source lake to outlet at Little Port Walter estuary on Baranoff Island, southeastern Alaska. Numbers and letters refer to RETURNS sampling stations.

The 30-m-high waterfall, located 1200 m upstream from the mouth of the stream, prevents further upstream migration by salmon, thus dividing Sashin Creek into a salmon-spawning section and a non-salmon control section (Fig. 2). A 15-m-high falls further subdivides the upper (control) section. Fish movement is restricted to downward migration through the two falls. Sashin Creek resident fishes are thus separated into three sections: the upper two sections comprise the non-salmon control section and the lowermost section comprises the salmon-spawning section (Fig. 2).

A unique aspect of Sashin Creek is the population of rainbow trout, planted in Sashin and Round lakes by Little Port Walter herring plant personnel in the 1920's. These fish reside in the source lakes as well as in all sections of the stream. The rainbow trout were originally steelhead, or anadromous rainbow trout. Some of the rainbow trout from both above (including the lakes) and below the 30-m falls have retained anadromy, migrating out to sea as 15- to 18-cm, 2- to 3-yr-old smolts in April to May. Others that are nonanadromous and that mature at 20 cm maintain the reproducing population in the control section (W. R. Heard, NMFS, Auke Bay Laboratory, Juneau, AK, pers. comm.).

In addition to the rainbow trout, the spawning section has resident Dolly Varden, coastrange sculpin (*Cottus aleuticus*), and coho salmon (*O. kisutch*) juveniles. The dominant anadromous species is pink salmon (*O. gorbuscha*). Annually about 30 000 adult pink salmon return to Sashin Creek to spawn and die. Peak spawning occurs in August and September. Pink salmon fry emerge from the gravel and migrate to sea during the following March and April. Because of the brief freshwater stage of pink salmon juveniles, nutrients released by decaying carcasses are more likely to benefit the other resident fish species of Sashin Creek.

Brickell and Goering (1970) measured nutrient concentrations in both the lower 1200 m of Sashin Creek and above the 30-m falls from the end of August (prespawning period) to the end of October (postspawning). They found NH_4^+ concentrations below 2 μM both above and below the 30-m falls prior to spawning. Following the spawning, commencing with the appearance of carcasses in the stream, NH_4^+ increased in concentration with time and in the downstream direction. The peak NH_4^+ level, near 8 μM, occurred near the mouth of the stream at the end of September. They observed that most of the carcasses were flushed out of the stream by the end of September during heavy rains. Dissolved organic N (DON) exhibited a pattern similar to NH_4^+. The background DON level in the control section was below 6 μM. The DON peak in the spawning section was coincident with the NH_4^+ peak and was near 18 μM. The peak of dissolved nutrients measured by Brickell and Goering (1970) was limited to about 1 mo in Sashin Creek. In comparison, nutrient retention in lakes is generally on the order of years depending on flushing rate and other loss terms.

Materials and Methods

Sampling

Four sampling stations were established in Sashin Creek (Fig. 2), stations 1 and 2 in the lower 1200-m salmon spawning section and stations 3 and 4 in the upper non-salmon control sections. These stations were sampled for stream biota during three sampling trips. The three trips were timed to correspond with nutrient conditions prior to arrival of returning adult salmon, 23 – 24 July 1985, after the peak of nutrient loading observed by Brickell and Goering (1970), 4 – 5 November 1985, and at the time of fry emergence, 4 – 5 April 1986, to determine the seasonal extent of MDN in primary producers and to facilitate the sampling of different organisms.

Baited minnow traps were used to collect resident fishes during each sampling trip. All aquatic insects and turbellarians that were found and collected came from beneath rocks. Fish, turbellarian, insect, leaf litter, and loose salmon egg samples were desiccated over silica gel (SiO) (July trip) or frozen and returned to the laboratory for isotopic analysis.

Periphyton (benthic algae) was collected (when available) at each station and at additional sites, where patches of periphyton occurred (ancillary stations A through D; Fig. 2.), from rocks collected in the stream by scraping off algae (mostly filamentous green algae) followed by rinsing into whirlpac bags. The periphyton was then concentrated onto precombusted (400°C) Gelman GFC glass-fiber filters (July) or precombusted (500°C) Whatman QM-1 quartz-fiber filters. Filter-trapped material was either desiccated over silica gel or frozen. All samples were stored frozen (– 20°) until analysis for $\delta^{15}N$ and $\delta^{13}C$. Samples were thawed for sorting and fork length measurement of fishes prior to preparation for mass spectrometry.

Sample Preparation and Mass Spectrometry

Samples were refrozen, freeze dried (Labconco Freeze Dryer 5) and ground (Thomas-Wiley intermediate dry mill) to a fine powder. Approximately 25 mg dry weight for fishes, turbellarians, and caddis fly larvae and 100 mg dry weight for other insects and plant material was subsampled per combustion for isotopic analysis. This mass requirement sometimes necessitated the pooling of organisms. Only fishes and a few larger caddis fly larvae could be analyzed individually. When possible, replicate subsamples were made. The number of replicates is indicated in Tables 1 and 2. The population averages of mean subsample values from individual fish are reported in Table 3. Each fish was analyzed one to seven times. Subsamples were ground together with 1.5 g of precombusted (900°C) Coleman Cuprox and loaded into Vycor or quartz tubing with approximately 200 mg of precombusted (400°C) silver foil. Loaded samples were evacuated under vacuum (<100 μPa), sealed, and combusted for 2 h at 450°C followed by 2 h at 850°C. Samples were cooled slowly (overnight with muffle furnace door closed) to minimize sample loss. CO_2 and N_2 was cryogenically distilled from each combusted sample (sample preparation methods and sources of error reviewed by Owens 1987).

Isotope ratios were determined with a VG Isogas SIRA-9 dual-inlet, triple-collector, isotope ratio mass spectrometer. Two secondary standards (one of which was derived from the same combustion and cryodistillation method as the samples) were run with samples during each mass spectrometer run against Matheson and Gollub reference gases for N_2 and CO_2, respectively.

The isotope ratio is reported in delta notation, defined as the per mil deviation from the recognized isotope standard, atmospheric N_2 for $^{15}N/^{14}N$ and Peedee Belemnite (PDB limestone) for $^{13}C/^{12}C$, by the following formula:

$$\delta^{B}X = \frac{{}^{B}X/{}^{A}X_{\text{sample}} - {}^{B}X/{}^{A}X_{\text{standard}}}{{}^{B}X/{}^{A}X_{\text{standard}}} \times 1000 \text{ per mil}$$

where X is the element (N or C), A is the major isotope mass number, ^{14}N or ^{12}C, and B is the minor isotope mass number, ^{15}N or ^{13}C (after Craig 1957). Ranges of observed environmental values for $\delta^{15}N$ are from 0 to near $+20$ and for $\delta^{13}C$ from 0 to -50. The negative range of $\delta^{13}C$ values reflects the relative enrichment of ^{13}C in the PDB standard. Precision is 0.1 and 0.2 per mil for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Results and Discussion

The basis for determining the significance of MDN was the $\delta^{15}N$ difference between control and spawning section food webs of Sashin Creek. Interpretation of $\delta^{15}N$ was based on application of the observed values to the mixing model (Fig. 1). In addition to autochthonous production (e.g. periphyton), allochthonous inputs such as leaf litter and salmon (primarily eggs and fry because carcasses tend to be washed out of the system, Brickell and Goering 1970) had the potential for making a contribution of fixed nutrients to the system. The results and interpretation pertaining to allochthonous inputs are presented first because some of these may affect the whole system. Each trophic level is then presented on a comparative basis, control versus spawning section. The results are synthesized into a graphic model that illustrates the differences and similarities in C and N isotope ratios of food webs at the four Sashin Creek stations in the isotopic food webs section.

TABLE 1. Isotope ratios of periphyton. Samples from stations marked with an asterisk were *Fontinalis*; others were algae. SD = replication standard deviation (reported as 0.1 (precision) if SD was less) and *n* = number of replicate analyses; separate lines indicate different samples; stations listed in downstream order within each section.

Station	$\delta^{15}N$	SD	*n*	$\delta^{13}C$	SD	*n*
			Control section			
July 1985						
4	+0.2	—	1	−28.9	0.2	2
D	−0.1	1.0	2	−22.6	0.1	4
3	−2.0	0.2	5	−22.4	0.1	3
3	+1.8	0.3	3	−29.2	0.1	8
November 1985						
4	+0.5	0.5	4	−27.8	0.1	3
4	+1.5	0.1	2	−34.3	0.8	2
D	+0.2	0.3	2	−22.1	0.1	2
D	+0.5	0.1	3	−24.0	0.1	2
3	+1.0	0.1	3	−26.6	0.1	5
3	+0.5	—	1	−23.2	0.1	5
April 1986						
4	+1.5	0.1	3	−39.4	—	1
4	+1.1	0.6	3	—	—	—
D	−0.5	0.2	2	−20.6	—	1
3	+0.9	—	1	−27.3	0.2	3
			Spawning section			
July 1985						
2	—	—	—	−17.3	0.1	3
2	+3.8	—	1	−15.8	0.2	8
A	+2.2	0.1	4	−16.4	0.1	8
November 1985						
2	+1.4	0.2	3	−16.2	0.1	7
1	+5.4	—	1	−23.7	0.1	2
C	+6.2	0.4	3	−22.6	0.4	7
B	+6.3	—	1	—	—	—
B*	+7.0	0.2	2	−16.8	—	1
April 1986						
2	+0.6	0.2	4	−17.1	0.2	6
2	—	—	—	−18.6	0.1	4
C	+2.4	0.1	2	—	—	—
C*	+4.3	0.2	4	−31.8	0.1	4
A	+3.3	0.1	4	−18.6	0.5	3

Allochthonous sources

Allochthonous sources of organic matter include eggs and fry (prior to feeding), which are wholly of marine origin, and terrestrial production detritus such as leaf litter. Alder (*Alnus rubra*) leaf litter collected in November from control and spawning sections had a $\delta^{15}N$ of -0.7 and $\delta^{13}C$ of -29.1 at station 3 and a $\delta^{15}N$ of -1.0 and $\delta^{13}C$ of -27.2 at station 2. $\delta^{15}N$ values near 0 are probably due to the small isotope effect in symbiotic N_2 fixation within the alder tree (Hoering and Ford 1960; Delwiche and Steyn 1970).

Marine allochthonous organic matter available to the Sashin Creek carnivores and scavengers includes salmon eggs lost during spawning, developing eggs which might be dislodged during development, and fry emerging from the gravel. Loose salmon eggs collected in November had a $\delta^{15}N$ of $+11.6$ (SD $= 0.5$, $n = 5$ eggs) and $\delta^{13}C$ of -23.4 (SD $= 0.7$, $n = 5$ eggs). The $\delta^{15}N$ for developing embryos was $+12.5$ (pool of

11 eggs, one sampled each week for 11 wk during incubation, P. L. Parker, unpubl. data).

Periphyton

Periphyton from the control section had $\delta^{15}N$ values near 0 (range -2.0 to $+1.8$; Table 1). The more positive periphyton $\delta^{15}N$ values from the spawning section (range $+0.6$ to $+7.0$; Table 1) compared with periphyton from the control section are ascribed to the input of MDN. The $\delta^{15}N$ of periphyton in the spawning section was relatively low in July but nevertheless was higher than control section periphyton at this time. The November $\delta^{15}N$ values of periphyton from the spawning section were the highest observed during this study, with all values $>+6$ below station 1. With the exception of station 2, these control section $\delta^{15}N$ values were higher than the periphyton $\delta^{15}N$ values obtained for July or April.

The $\delta^{15}N$ values of periphyton from below station 1 in November were $\geqslant +6.2$, corresponding to $\geqslant 90\%$ MDN according to the isotope mixing model (Fig. 1). This compares with periphyton ($\delta^{15}N = +1.4$; ~20% MDN) from station 2, located just below the falls where there is a minor input of dissolved marine N (Brickell and Goering 1970), and with control section periphyton ($\delta^{15}N = 0 \pm 2$ throughout study). Periphyton from below station 1 in the April and July sampling have $\delta^{15}N$ values ranging from $+2.2$ to $+4.3$ corresponding to about 30 – 60% MDN. This may result from retention of marine N by the plants themselves or from regenerated N of marine origin. The isotopic evidence suggests that the lower Sashin Creek section periphyton are very dependent on MDN, with a MDN contribution to the N budget of >90% following spawning and near half at other times.

The $\delta^{13}C$ values for periphyton collected from the control section ranged from -39.4 to -20.6 (Table 1). Two isotopically distinct sources of periphyton C came from each of the two tributaries. Periphyton $\delta^{13}C$ values at station 4 (just below Sashin Lake) ranged from -39.4 to -27.8, while periphyton from station D on Round Creek had $\delta^{13}C$ values from -24.0 to -20.6. There were intermediate $\delta^{13}C$ values for periphyton (-29.2 to -22.4) at station 3 (located below the confluence). Periphyton $\delta^{13}C$ values from the spawning section ranged from -31.8 to -15.8 during this study. Most of these were heavier than -20 which contrasts with the control section values that were all lighter than -20.

Invertebrates

July insect samples had similar $\delta^{15}N$ values below and above the 30-m falls (Table 2) although the low abundance of insects available then necessitated pooling of the insects in each sample. The insects could represent a range of trophic levels, thereby obscuring the isotopic signature of the N source. The two insect samples collected in July at station 3 may reflect such trophic level differences.

The larger number of insects sampled in April due to the greater availability of insects allowed a taxonomic separation into potential functional groups: caddis fly larvae primarily as herbivores and stonefly nymphs as omnivores. Caddis fly larvae from stations 1 and 2 had mean $\delta^{15}N$ values of $+10.0$ and $+7.3$, respectively. This compared with $+4.8$ from the control section (Table 2). The $\delta^{15}N$ values of stonefly nymphs collected during April were $+12.8$ at station 1 compared with $+5.1$ in the control section.

TABLE 2. Isotope ratios of insects (SFN = stonefly nymphs, CFL = caddis fly larvae) and turbellarians. SD = replication standard deviation (reported as 0.1 (precision) if SD was less) and n = number of replicate analyses; separate lines indicate different samples; stations listed in downstream order within each section.

Station	$\delta^{15}N$	SD	n	$\delta^{13}C$	SD	n	Taxon
Control section							
Insects							
July 1985							
4	+15.3	0.2	2	−33.4	0.1	6	All
3	+4.7	0.2	2	−29.4	0.5	6	All
3	+18.0	0.2	2	−29.7	0.3	5	All
April 1986							
3	+5.1	0.4	4	−30.0	0.1	4	SFN
3	+5.3	—	1	−30.5	—	1	All
3	+4.8	1.5	4	−28.9	2.3	10	CFL
Turbellarians							
July 1985							
4	—	—	—	−32.6	—	1	
Spawning section							
Insects							
July 1985							
2	—	—	—	−26.4	0.2	3	All
1	+15.2	0.2	2	−23.6	0.2	4	All
1	—	—	—	−28.3	0.2	4	All
April 1986							
2	+7.3	1.0	9	−21.8	1.3	8	CFL
1	+5.1	1.0	2	−27.4	0.7	2	All
1	+12.8	0.2	2	−25.8	1.8	9	SFN
1	+10.0	0.8	7	−23.5	0.9	8	CFL
Turbellarians							
July 1985							
2	—	—	—	−24.5	—	1	
2	—	—	—	−22.9	0.1	3	
1	+17.3	0.1	2	−23.7	0.1	5	
April 1986							
2	+14.7	0.2	2	−23.9	0.2	3	
2	+13.3	0.1	2	−23.7	0.1	3	

The low $\delta^{15}N$ values for insects from the control sections of Sashin Creek ($+4.7$ to $+5.3$) were near the expected value ($+3$) for herbivores receiving no marine N (0% MDN in the $\delta^{15}N$ mixing model, Fig. 1). The slightly higher than expected $\delta^{15}N$ values may have been from predatory insects in a portion of the sample causing the expected trophic enrichment in ^{15}N. Caddis fly larvae sampled in April at station 1 had $\delta^{15}N$ values of $+10.0$ corresponding to herbivores with 100% MDN in the $\delta^{15}N$ mixing model. They contained about 50% MDN at station 2 ($\delta^{15}N = +7.3$). These high $\delta^{15}N$ values in April may be due to retention of N during overwintering as well as from grazing on periphyton or microbial decomposers (e.g. fungi) residing on dead eggs and fishes. Caddis fly larvae feeding on the surface of dead fishes have been observed during snorkeling in salmon spawning habitats (T. C. Kline, pers. comm.). Similarly, stonefly nymphs ($\delta^{15}N = +12.8$, station 1) may be consuming fish components (carcasses or eggs) as well as periphyton.

The $\delta^{13}C$ values of spawning section aquatic insects ranged from -28.3 to -21.8, while $\delta^{13}C$ values of insects from the control

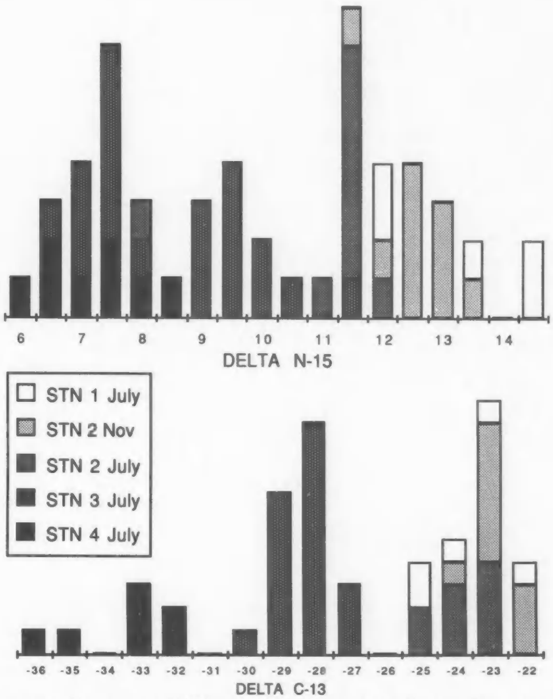

FIG. 3. Histograms of $\delta^{15}N$ and $\delta^{13}C$ values of individual rainbow trout from stations and dates as indicated in legend.

TABLE 3. Isotope ratios of fishes. Asterisks indicate distributions histogrammed in Fig. 3; n = number of fish; July station 3 rainbow trout population separated into two modes; stations listed in downstream order within each section.

Station	$\delta^{15}N$	n	$\delta^{13}C$	n
		Control section		
Rainbow trout				
(*Oncorhynchus mykiss*)				
July 1985				
4*	+7.4	7	−33.0	7
3*	+7.5	10	−28.1	10
3*	+10.0	11	−27.6	11
November 1985				
4	+7.2	3	−30.8	3
3	+8.0	3	−26.1	3
April 1986				
3	+9.1	2	−26.2	2
		Spawning section		
Rainbow trout				
(*Oncorhynchus mykiss*)				
July 1985				
2*	+11.3	9	−23.3	9
1*	+13.4	5	−23.3	5
November 1985				
2*	+12.8	10	−22.3	10
1	+13.8	2	−22.1	2
April 1986				
1	+12.9	1	−22.1	1
Dolly Varden				
(*Salvelinus malma*)				
July 1985				
2	+10.9	2	−24.4	2
1	+13.5	3	−21.2	3
November 1985				
1	+12.2	1	−22.2	1
April 1986				
1	+12.9	1	−22.7	1
Coho salmon				
(*Oncorhynchus kisutch*)				
July 1985				
2	+9.0	2	−24.5	2
1	+12.0	3	−24.0	3
November 1985				
2	+11.4	1	−24.2	1
1	+13.5	1	−23.6	1
Coast range sculpin				
(*Cottus aleuticus*)				
July 1985				
2	+13.1	1	−23.6	1
November 1985				
1	+13.0	1	−23.6	1

section ranged from −33.4 to −28.9 (Table 2). This evidence suggests that insects are selectively feeding on organic matter that is isotopically light in all sections of the stream (compare $\delta^{13}C$ values of insects with available periphyton $\delta^{13}C$ range at each station). Furthermore, control section insects had ^{13}C-depleted Sashin Lake C similar in value to that found in the station 4 periphyton, suggesting the importance of respired C in the aquatic insect food chain in the control section of Sashin Creek. Control section turbellarians (Table 2) had $\delta^{13}C$ values similar to insects. The high $\delta^{15}N$ in spawning section turbellarians (Table 2) suggests that they may be consuming marine N (e.g. scavenging salmon eggs or carcasses).

Fishes

Rainbow trout

Rainbow trout $\delta^{15}N$ values at station 3 (July) had a bimodal distribution (Fig. 3). Station 4 rainbow trout (July) and the lower mode of station 3 (July) rainbow trout had mean $\delta^{15}N$ values of +7.4 and +7.5 (Table 3), respectively. The higher mode of July station 3 rainbow trout was +10.0 (Table 3). Rainbow trout from station 4 in July ranged from 70 to 125 mm in length. All but one (115 mm) of the station 3 lower $\delta^{15}N$ mode rainbow trout were ≤100 mm. The station 3 upper $\delta^{15}N$ mode rainbow trout ranged from 101 to 148 mm. The longer length for the higher $\delta^{15}N$ mode trout suggests that these trout were secondary carnivores.

The lower $\delta^{15}N$ mode from station 3 and the mean $\delta^{15}N$ value of station 4 rainbow trout approximate the $\delta^{15}N$ mixing model predicted $\delta^{15}N$ of +6 for primary carnivores based on no marine N input. The higher $\delta^{15}N$ mode of larger rainbow trout (>100 mm) from station 3 approximates the model-expected value for secondary carnivores (+9) based on no marine N input. The $\delta^{15}N$ values for rainbow trout of station 3 were partially correlated with length (r = 0.7); in comparison, spawning section rainbow trout $\delta^{15}N$ values were not correlated with length ($r =$ 0.1).

In July, rainbow trout from station 4 had $\delta^{13}C$ values which were about 5 per mil more negative than station 3. The unimodality of the station 3 rainbow trout $\delta^{13}C$ values (cf. the $\delta^{15}N$ bimodality; see Fig. 3) was demonstrated by comparing the mean $\delta^{13}C$ values corresponding to each $\delta^{15}N$ mode. Mean station 3 rainbow trout $\delta^{13}C$ values were −28.2 and −27.6 for the lower and higher $\delta^{15}N$ modes, respectively. The difference in these two $\delta^{13}C$ values was insignificant ($p > 0.10$, *t*-test).

Control section rainbow trout $\delta^{15}N$ and $\delta^{13}C$ values in November and April were similar to the mean of the larger sample size collected in July (Table 3). Sample size was insufficient to determine whether the bimodal $\delta^{15}N$ distribution from July occurred in November or April at station 3.

Three rainbow trout samples from the spawning section (Table 3) are histogrammed in Fig. 3. The large ($n = 10$) November station 2 sample mean ($\delta^{15}N = 12.8$) corresponds to 100% MDN in the mixing model. Station 1 rainbow trout from November and April also fit the model (at 100% MDN), with individual $\delta^{15}N$ values that ranged from +12.9 to +14.1. The relatively low mean $\delta^{15}N$ of +11.3 (the mean would be +11.7 if a single anomalous +8.4 rainbow trout was eliminated) observed at station 2 for rainbow trout in July is within 2 per mil of the expected value (+13) but fits in the $\delta^{15}N$ mixing model at about 75% MDN.

Although a variety of fishes were sampled in the control section (Table 3), rainbow trout was the only fish found in both control and spawning sections and is thus the only aquatic top consumer that can be applied to the full range of the mixing model (0 – 100% MDN). In general, the rainbow trout from the spawning section had elevated $\delta^{15}N$ values (~5 per mil) in comparison with those found in the control section (see Fig. 3). Mean rainbow trout $\delta^{15}N$ values from station 2 in July, station 2 in November, and station 1 in July were +11.3, +12.8, and +13.4, respectively, compared with station 4 in July and the two $\delta^{15}N$ modes of station 3 in July, which were +7.4, +7.5, and +10.0, respectively. The difference in $\delta^{15}N$ values between the five groups, pooled July station 3, July station 4, July station 2, November station 2, and July station 1, was significant ($p < 0.0001$, one-way ANOVA). The difference between station 2 July and November rainbow trout $\delta^{15}N$ values was significant as were the differences between July station 2 and station 1 rainbow trout $\delta^{15}N$ values ($p < 0.005$, *t*-test).

Similar statistical analyses were performed on $\delta^{13}C$ data. The five rainbow trout groups, July station 4, July station 3, July station 2, November station 2, and July station 1, were significantly different ($p < 0.0001$, one-way ANOVA; see Fig. 3). The July rainbow trout control section $\delta^{13}C$ values, station 1 and station 2, were not significantly different ($p > 0.4$, *t*-test; see Fig. 3). Station 2 rainbow trout $\delta^{13}C$ values were significantly different between July and November ($p < 0.005$, *t*-test; see Fig. 3).

Other fishes

The ultimate goal is to show the importance of MDN at the ecosystem level and this includes species that may not occur in areas not affected by salmon, particularly juvenile anadromous fishes that may benefit from a nutrient feedback mechanism between adults and their offspring (Mathisen 1972). Fishes other than rainbow trout from the spawning section had $\delta^{15}N$ values near +13 ± 2 per mil. These fishes had $\delta^{13}C$ values that also fell in the same range as the rainbow trout. The only unusual datum was from a coho salmon ($\delta^{15}N = +7.8$). However, there was a slightly heavier $\delta^{15}N$ value observed for a spawning section rainbow trout ($\delta^{15}N = +8.4$).

Isotopic Food Webs

Two pathways for utilization of MDN by foodwebs yielding fishes in Sashin Creek are postulated: (1) excretion by adult salmon and decomposition of carcasses resulting in the release of dissolved N and other nutrients which are utilized by primary producers and then transferred up a food chain to resident fishes and (2) direct utilization of organic marine N by predation on salmon eggs and fry by resident fishes and scavenging of carcasses by invertebrates. The high $\delta^{15}N$ signal in spawning section biota (Tables 1 – 3) is evidence that MDN is important irrespective of pathway. Because N and C geochemical cycles are decoupled during remineralization, the $\delta^{13}C$ of marine organic matter would not be conserved. However, if marine organic matter such as salmon eggs is consumed, then marine C is conserved and the $\delta^{13}C$ of the eggs may be used to identify marine C and, indirectly, N that was utilized by organisms feeding on eggs. A major rationale for making $\delta^{13}C$ determinations was to attempt to differentiate potential pathways for the utilization of MDN.

The very negative $\delta^{13}C$ values of biota obtained from the uppermost part of Sashin Creek (station 4) are evidence that respired C may be in important C source in Sashin Lake. The C is probably allochthonous, from isotopically light terrestrial detritus (e.g. alder leaf litter, $\delta^{13}C = -28.2$), released as CO_2 during decomposition. Fixation of respired CO_2 yields organic matter further depleted in ^{13}C because of isotopic discrimination during photosynthesis. Rau (1978, 1980) reported $\delta^{13}C$ as low as −45.9 for phytoplankton in Findley Lake, Washington, which he attributed to photosynthetic fractionation of recycled CO_2. The periphyton $\delta^{13}C$ values of approximately −35 (range −27.8 to −39.4) from Sashin Creek near the outlet of Sashin Lake (station 4) indicate that periphyton utilize a mixture of respired C and atmospheric CO_2, similar to Findley Lake periphyton $\delta^{13}C$ values. Notably, the isotopically light C at station 4 is evident in the entire food web including the rainbow trout. The organisms deriving their C from this part of the system are distinct from sections of Sashin Creek located downstream of station 4 below the 15-m falls. These lower section periphyton are apparently not significantly affected by the respired C.

Rainbow trout from the salmon spawning section of Sashin Creek had different isotopic trends than those from the control section. The $\delta^{13}C$ values were much narrower in range, with mean values near −23 in July and −22 in November compared with means near −28 and −33 for trout collected in July from stations 3 and 4, respectively. The $\delta^{13}C$ values for rainbow trout collected at other times had similar $\delta^{13}C$ values at each station. Other fishes collected from the spawning section had $\delta^{13}C$ values ranging from −22 to −26, suggesting a C source very similar to that of rainbow trout from the same area. These were also distinct from rainbow trout from the control section. The spawning section $\delta^{15}N$ values of rainbow trout ranged from +7.8 to +14.5, much more positive than rainbow trout $\delta^{15}N$ values found in the control section. Because both the N and C for entire food webs from above, between, and below the two falls were isotopically distinct, it can be concluded that these three sections of the stream are partially independent ecosystems with the spawning section dependent on marine nutrients transported in by returning adult salmon. Because very negative

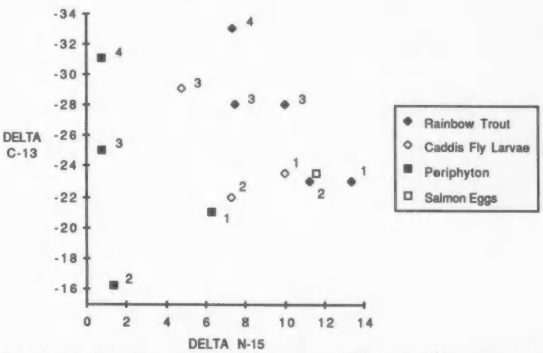

FIG. 4. Dual-isotope ratio plot of mean $\delta^{15}N$ and $\delta^{13}C$ values for selected Sashin Creek biota. Periphyton values are from November, 1985 (maximum $\delta^{15}N$ observed in control section; station 1 value incorporates ancillary stations A, B, and C). Caddis fly larvae values are from April 1986 (abundant then). Rainbow trout are from July 1985 (largest sampling; station 3 separated into two $\delta^{15}N$ modes). Salmon eggs are from November 1985. Numbers indicate stations.

$\delta^{13}C$ values were never present in spawning section biota, it can be concluded that biogenic C inputs from above the 30-m falls are biogeochemically insignificant there.

The advantage of the dual-isotope technique is best seen by plotting $\delta^{15}N$ values against $\delta^{13}C$ values on a cartesian plane, as done by Peterson et al. (1985, 1986) and Peterson and Howarth (1987). The main rationale for the selection of biota in the dual-isotope plot in Fig. 4 was the seasonal availability of the organisms. Peak observed $\delta^{15}N$ values of periphyton that occurred in November are plotted as potential sources of organic matter when MDN was most likely to be significant. The position of the periphyton values on the plot compares well with the other MDN source for stream consumers, salmon eggs. Because of the a priori trophic fractionations of +3 for $\delta^{15}N$ and +1 for $\delta^{13}C$ (DeNiro and Epstein 1978; Fry and Sherr 1984), it is possible to estimate coordinates for consumers relative to potential forage items (i.e. a shift slightly down and to the right would indicate a trophic link in Fig. 4). Caddis fly larvae (only found in abundance in April) were selected as a consumer of periphyton to provide a linkage for remineralized MDN and forage for rainbow trout. The rainbow trout values selected for Fig. 4 were from July when the largest collection was made. Note that the two modes for station 3 are shown as distinct points with a relative positioning, suggesting a canabalistic role for the larger fish. Macrofauna (e.g. rainbow trout and caddis fly larve) average out seasonal fluctuations in isotopic abundance that may occur at the primary producer level (Wada et al. 1987). Thus the high $\delta^{15}N$ of station 1 and 2 caddis fly larvae (April) indicates the significance of MDN over a longer term than just the November $\delta^{15}N$ peak observed for periphyton. Furthermore, the observed caddis fly larvae isotope ratio values for stations 1, 2, and 3 (April) fit in as a potential diet for rainbow trout (July). The $\delta^{15}N$ and $\delta^{13}C$ values of higher trophic level organisms may well represent a true weighted mean value of useful, convertable to higher trophic level, production.

Comparison of the relative importance of three sources of forage for spawning section rainbow trout that correspond to three production sources, autochthonous production based on about 50% MDN (station 2), autochthonous production based on 100% MDN (station 1), and salmon eggs (and fry), is predicated on the a priori trophic fractionations of +3 for $\delta^{15}N$ and +1 for $\delta^{13}C$. Isotope ratio coordinates so predicted for rainbow trout feeding on station 1 and 2 caddis fly larvae and salmon eggs were more extreme than those observed. Therefore, a combination diet of caddis fly larvae (consumers of autochthonous production) and salmon eggs or fry is most likely. In comparison, the $\delta^{15}N$ and $\delta^{13}C$ values for turbellarians collected at station 2 in April (Table 2) would fit near the values expected for consumption of salmon eggs, suggesting a scavenger role. Thus, although salmon eggs and fry may be consumed by rainbow trout, providing a direct means of incorporating marine nutrients, the data suggest that at least part of the diet comes from autochthonous production based on MDN.

Comparison of the position of the biota in Fig. 4 shows the similarity in $\delta^{15}N$ values between stations 3 and 4 (note the extra trophic level at staion 3) as well as the dichotomy in $\delta^{13}C$ values. Similarly, comparison of stations 3 and 4 with stations 1 and 2 shows the difference in both $\delta^{15}N$ and $\delta^{13}C$. This reinforces the conclusion that the spawning section is biogeochemically distinct from the rest of the stream and the evidence suggests that the difference is due to the input of biogenic marine-derived nutrients.

This study suggests that marine biogenic N plays a significant role in the biogeochemical cycle of N in the section of Sashin Creek utilized by spawning anadromous Pacific salmon. $\delta^{15}N$ proved to be a useful tracer of MDN because no unusual fractionations or geochemical processes which alter ^{15}N abundance appear to take place in Sashin Creek (cf. Antarctic dry valley lakes; Wada et al. 1981, 1984). Possibly the rapid flushing of Sashin Creek prevents geochemical processes from occurring that would enrich the DIN pool in ^{15}N, thus permitting the use of a $\delta^{15}N$ value of zero for the 0% MDN primary producer endmember.

It is probable that other elements transported upstream from the marine environment by returning salmon are important as well (Mathisen et al. 1988). These results imply that reduced input of marine-derived biogenic nutrients from salmon through reduction of stocks by fishing may affect coastal stream ecosystems. Artificial fertilization, to alleviate nutrient loss in lake systems (e.g. Stockner 1981, 1987), may be a possible replacement for reduced dissolved nutrient input, but would not substitute for eggs and carcasses that feed consumers and decomposers in lotic systems.

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Experimental Harvest Policies for a Mixed-Stock Fishery: Fraser River Sockeye Salmon, *Oncorhynchus nerka*

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We investigated harvest strategies aimed at rebuilding the less abundant stocks of Fraser River sockeye salmon, *Oncorhynchus nerka*. Monte Carlo simulations were run to estimate catch under four different harvest policy designs and three alternative parameterizations of the Ricker model. A pooled regression model was fit to 34 yr of spawner–recruit data from the 10 major stocks of Fraser sockeye. Compared with estimating separate parameters for each stock, the pooled regression model resulted in a more precise estimate of the Ricker a parameter (productivity at low stock sizes). Exploitation rate for maximum sustainable yield depends only on the a parameter and is thus well defined by the pooled regression even though the corresponding optimal escapement levels remain uncertain. A reduction in harvest rates to 70% from the current average 80% increased the simulated 40-yr catch by 31%. More extreme harvest-rate reductions, involving 50% exploitation rates on some stocks for four generations, allowed faster rebuilding and further increases in catch. Extreme harvest-rate reductions were necessary to obtain a 0.5 or greater probability of correctly detecting increased escapements, should the less-abundant runs increase as expected.

Nous avons étudié des stratégies de récolte qui permettraient de reconstituer les stocks les moins abondants de saumon sockeye, *Oncorhynchus nerka*, du fleuve Fraser. Nous avons effectué des simulations à l'aide de la méthode de Monte Carlo pour estimer les captures qui résulteraient de l'application de quatre stratégies de récolte différentes et de trois nouvelles façons de paramétrer le modèle de Ricker. Un modèle de régression prenant en compte les dix stocks principaux de sockeye du fleuve Fraser a été adapté à des données relatives à la quantité de géniteurs et au recrutement couvrant une période de 34 an. Ce modèle de régression combiné a donné une estimation plus précise du paramètre « a » de Ricker (productivité pour des stocks de petite taille) comparée aux résultats obtenus en estimant séparément les paramètres pour chacun des stocks. Le taux d'exploitation correspondant à un rendement soutenu maximum dépend seulement du paramètre « a » et se trouve donc bien défini par le modèle de régression combiné même si les niveaux d'échappées optimaux correspondants demeurent mal connus. Si les taux de récolte moyens actuels de 80 % sont réduits à 70 %, les captures pour la période simulée de 40 ans augmenteraient de 31 %. Si l'on réduit encore plus les taux de récolte, par exemple en considérant des taux d'exploitation de 50 % pour certains stocks durant quatre générations, la reconstitution des stocks serait accélérée et les captures augmenteraient encore plus. Il faut diminuer considérablement les taux de récolte avant d'obtenir une probabilité de 0,5 et plus de détecteur de façon sûre une augmentation de l'échappée et ce, à la condition que les stocks les moins abondants s'accroissent tel que prévu.

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The Fraser River, British Columbia, is one of the world's largest producers of sockeye salmon, *Oncorhynchus nerka*, with recent annual catches of 1 – 9 million fish. Yet these catches are small fractions of those from the large returns at the turn of the century, estimated by Ricker (1987) as at least 25 – 35 million fish. Since the signing of the Canada–U.S. Treaty on Pacific salmon in 1985, there has been growing interest in trying to increase the abundance of Fraser sockeye. The treaty motivates rebuilding and enhancement of salmon stocks by ensuring that each country receives benefits equal to the production of salmon originating in its own waters. Efforts to rebuild the stocks of Fraser sockeye are also spurred by the timely questioning of traditional attitudes about the maintenance of the cyclic pattern of abundance (cyclic dominance) in sockeye salmon (Walters and Staley 1987; Collie and Walters 1987; Eggers and Rogers 1987).

Most Fraser River sockeye mature as 4-yr-olds, a life cycle that leads to four relatively discrete populations (called lines) in each stock. The most abundant line in a given stock is referred to as the "dominant" line (e.g. 1986 Shuswap) and the next most abundant line as the "subdominant" (1987 Shuswap) with two "off-year" lines of quite low abundance. The terminology uses the most recent year in which the given line spawned to refer to any previous or subsequent run of that line. This persistent temporal pattern of dominant, subdominant, and off-years is called cyclic dominance.

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TABLE 1. Cycle–year/timing windows of selected Fraser River sockeye salmon lines. **Bold type** indicates dominant lines, regular type subdominant lines, and italic type off-year lines. "Pink" denotes comigration of pink salmon, with sockeye salmon through commercial fishing areas.

Cycle line years	Run-timing groups		
	Early	Middle	Late
1986	*Early Stuart*	Stellako Late Stuart Quesnel	**Shuswap** **Birkenhead**
1987	*Early Stuart*	**Stellako** Chilko *Late Stuart* *Quesnel*	Shuswap Pink
1988	Early Stuart	**Chilko** *Late Stuart* *Quesnel*	Weaver *Shuswap*
1989	**Early Stuart**	**Late Stuart** **Quesnel**	Weaver *Shuswap* Pink

Two sources of depensatory mortality (high mortality rate at low abundance) have been considered as causes of cyclic dominance. Neither the hypothesis of depensatory fishing nor that of depensatory predation in early life can be refuted with existing data. The causes and mechanisms of cyclic dominance will not be elucidated by reanalyzing past data, or by further detailed studies of particular life stages (e.g. Ricker 1941; Ward and Larkin 1964). The only definitive test of the mechanisms causing cyclic dominance is to experimentally attempt to increase the abundance of the small runs in cyclic populations.

In this paper we identify experimental harvesting designs that will distinguish man-induced from natural causes of cyclic dominance. We use recent data on the major stocks of Fraser River sockeye salmon to identify several alternative stock–recuitment models and construct a simulation model to estimate the increase in catches of various rebuilding strategies. This analysis extends that of Walters and Staley (1987) by refining the estimates of the stock–recruitment parameters and corresponding variances, by including a set of alternative models in simulating future performance, and by investigating a wider range of management options. Our study also extends Collie and Walters' (1987) detailed analysis of the Adams River stock by including the other major stocks of Fraser River sockeye.

One of the most difficult problems in fisheries management is to optimize the harvesting of mixed-stock fisheries. This problem is particularly acute in Fraser River sockeye because the major stocks cannot be harvested separately due to overlapping timings of migration through fishing areas and because the dominant lines of different stocks occur in different years (Table 1). The current policy of setting escapement targets for the dominant stock in each run-timing group may result in suboptimal harvest rates for other stocks in the same run-timing group, and may in fact contribute to the maintenance of cyclic dominance. The policies we investigate in this paper involve setting a harvest rate (catch/(adult returns)) for each run-timing group and searching for the rates that optimize yield over all substocks rather than just the dominant line of each stock.

Methods

Model Specification

The functional form we use in this study to predict the number of recruits (R_t) produced by spawning stock (S_t) in brood year t is the standard Ricker (1975) model

$$R_t = S_t \exp(a - bS_t) \tag{1}$$

in which a is related to the intrinsic rate of increase and $1/b$ is the number of spawners required for maximum recruitment. Collie and Walters (1987) tested a number of alternative functional forms for the stock–recruitment relationship, specifically for the Adams River stock, as well as the other major stocks considered here. The only alternative that appeared to fit the data better than the Ricker model was Larkin's (1971) model, which included interaction among cycle lines.

Despite its apparently better fit to the data, there are several problems with the Larkin model. First, the estimated productivity ($\hat{a}$, Walters and Staley 1987) is unrealistically high and would result in chaotic population fluctuations in the absence of harvesting. Stock–recruitment data from sockeye salmon in the Kvichak River, Alaska, have a pattern similar to the Fraser River data (Eggers and Rogers 1987). For both rivers there is statistical evidence that survival of a given year-class is influenced by the abundance of the previous year-class, but if this cross-year effect is included in the stock–recruitment model, $\hat{a}$ is unrealistically high. Estimates of the a parameter are positively correlated with estimates of the cross-year effects; therefore if a is overestimated, the cross-year effects are likely to be overestimated as well.

Second, the Larkin model is based on the hypothesis that freshwater survival is depensatory. However, for stocks in which smolts have been enumerated, there is no empirical evidence that egg-to-smolt or smolt-to-adult mortality is depensatory (Ricker 1941; Eggers and Rogers 1987). Furthermore, the Larkin model, as fit by Collie and Walters (1987), indicates that for all but two of the major Fraser River stocks, the best harvest policy is one of equal escapements for all lines of each stock.

Another model, which has been used by the Pacific Salmon Commission (PSC) to predict future run sizes of Fraser sockeye, it one in which a different stock–recruitment relationship is estimated for each line of the 4-yr cycle. A problem with this model is that it assumes innate differences in productivity or survival among the lines, but in fact, the pattern of dominance has shifted lines since 1900. Walters and Staley (1987) showed that apparent differences in stock–recruitment parameter estimates among cycle lines are likely to have arisen by chance and that the estimated relationships are biased because of the few observations from each line.

Given the shortcomings of the Larkin and PSC models, we restricted our attention to the most parsimonious functional form, the Ricker model. The confidence regions of the estimated Ricker parameters were used to identify alternative parameter combinations which reflect uncertainty about the mechanisms of density-dependent population regulation. Inclusion of a model with a high b value (strong density dependence) will mimic the low catches predicted by the Larkin and PSC models, but will not simulate cyclic dominance patterns. Cyclic dominance could be simulated with the Ricker model if depensatory fishing were included.

Historical Data Base

Recruitment and escapement data for brood years (1948–81 were compiled by Wayne Saito of the Department of Fisheries

TABLE 2. Fraser River sockeye stock–recruitment parameters as estimated by pooled regression method. All escapements are in thousands of effective females. Max. *R* is the escapement that generates maximum recruitment ($1/b_i$); Opt. *R* is the escapement that generates maximum yield (Ricker 1975). Numbers in the best-fit column are regression estimates except Quesnel for which the Max. *R* estimate is based on spawning capacity. The weak and strong d.d. columns are 90% confidence limits of the parameter estimates, except Quesnel, Late Stuart, and Weaver for which Max. *R* estimates are based on lake capacity (Ian Williams, Pacific Biological Station, Nanaimo, B.C., pers. comm.).

	Model					
	Weak d.d.		Best fit		Strong d.d.	
Escapement for:	Max. *R*	Opt. *R*	Max. *R*	Opt. *R*	Max. *R*	Opt. *R*
Early Stuart	515	348	188	132	115	85
Early Misc.	199	132	118	81	84	61
Quesnel	2049	1301	1031	695	893	631
Late Stuart	3571	2352	410	285	134	97
Chilko	1515	1036	549	394	337	252
Stellako	266	179	145	102	100	73
Birkenhead	820	563	124	90	67	50
Shuswap	4545	3211	1515	1120	909	696
Weaver	318	223	43	32	22	16
Late Misc.	50	35	34	25	26	20
Common *a* value	2.49		2.63		2.77	

and Oceans (DFO), New Westminster, B.C. For management purposes, the runs of Fraser River sockeye have been aggregated by DFO into 10 major stocks (Table 2). The Early Miscellaneous group includes the Nadina, Gates, Upper Pitt, Bowron, Fennell, Raft, Seymour, Early Chilko, and Scotch Creek stocks. Quesnel includes the Horsefly and Mitchell rivers; Shuswap includes the Lower Adams and Lower Shuswap rivers. The Weaver data include escapements to the artificial spawning channel since 1965. The Late Miscellaneous group includes the Cultus Lake, Harrison, and Portage Creek stocks. The stocks are mainly aggregated geographically (Fig. 1) except the Early and Late Miscellaneous groups, which are collections of small stocks with similar migration times.

In this analysis, as in Walters and Staley (1987) and Collie and Walters (1987), recruitment (R_t) is the number of adult sockeye produced by escapement (S_t). The abundance data include a mixture of ages; in the Fraser River, most adult sockeye mature at age 4, some at age 5, and very few at age 6. Recruitment is thus a sum of fish returning at different ages. "Jacks" (precocious males that return at age 3) were omitted from this study because they are not important in the commercial fishery and because the number of jacks in a given escapement has no demonstrable effect on the number of recruits per spawner. Escapement (S_t) is the number of females times the percent that successfully spawn (>90%).

Stock–Recruitment Parameter Estimation

We used a pooled regression approach as described by Kmenta (1971) and applied to coho salmon (*Oncorhynchus kisutch*) by Anderson and Wilen (1985). The advantage of the pooled approach, apart from doing 10 regressions at once, is that it allows parameters to be shared among substocks. The methodology and terminology were described in detail by Anderson and Wilen (1985) and are only summarized here. The Ricker model (Eq. 1) is linearized by taking logarithms such that the dependent variable in the regression is $y_{it} = \ln(R_{it}/S_{it})$. In matrix notation, the regression equation is

$$(2) \quad y = X\beta + e$$

where the vector y contains a subvector of $T = 34$ annual observations (t) for each of the $N = 10$ stocks (i). Matrix X consists of ones, zeros and escapements (S_{it}) arranged in blocks according to which parameters are assumed shared among stocks. Vector β contains the stock–recruitment parameters (a_i, b_i) and vector e contains the residual errors.

A three-step regression procedure is used to correct for the fact that the residuals, e_{it}, may be autocorrelated in time, cross-correlated among stocks, and have different variances for different stocks (heteroscedastic), conditions which cause the parameter estimates to be unbiased but not minimum variance. (1) The residuals of the initial regression (Eq. 2) are used to estimate first-order autocorrelation coefficients, ρ_i. (2) The variables y and X are transformed by first differencing using $\hat{e}_{it}$, a new regression performed, and the new residuals used to estimate the covariance in residuals among stocks, σ_{ij}^2. (3) The $\hat{\rho}_i$ and $\hat{\sigma}_{ij}^2$ are used to construct a weighting matrix, Ω, and an asymptotically efficient estimate of β is given by the generalized least-squares estimator

$$(3) \quad \beta = (X'\hat{\Omega}^{-1}X)^{-1}(X'\hat{\Omega}^{-1}y)$$

The solution of (Eq. 3) can be simplified with a procedure given by Silvey (1975, p. 54).

We examined two hypotheses concerning the number of parameters shared among stocks. The null hypothesis (H_0) is that the stocks share a common a parameter but have unique b parameters. The rationale for this hypothesis is that a, being related to the intrinsic rate of increase, is more likely to be similar among stocks whereas b is related to habitat capacity and is more likely to be different among stocks. The alternative hypothesis (H_1) is that both a and b are different among stocks. An F statistic was calculated to test whether the sum of squared residuals (SS) is significantly reduced by the extra parameters of H_1:

$$(4) \quad F = \frac{(\mathrm{SS}_0 - \mathrm{SS}_1)/(\mathrm{df}_0 - \mathrm{df}_1)}{\mathrm{SS}_1/\mathrm{df}_1}$$

where df_0 and df_1 are the degrees of freedom of the aggregated $[N(T-1)-1]$ and disaggregated models $[N(T-2)]$, respectively (Anderson and Wilen 1985).

Individual $100(1-\alpha)\%$ confidence intervals (CI_k) for the stock–recruitment parameters ($\hat{\beta}_k$) were calculated as

$$(5) \quad \mathrm{CI}_k = \hat{\beta}_k \pm t(\mathrm{df},\alpha)\,(c_{kk}\,\mathrm{SS}/\mathrm{df})^{0.5}$$

where c_{kk} is the kth diagonal element of $(X'\hat{\Omega}^{-1}X)^{-1}$. Because of correlation among the parameters, the joint confidence region is generally different than the volume defined by the individual confidence intervals. A joint $100(1-\alpha)\%$ confidence region for all K parameters is described by

$$(6) \quad (\hat{\beta}-B)'X'\hat{\Omega}^{-1}X(\hat{\beta}-B) \leqslant F(K,\mathrm{df},\alpha)\,K\,\mathrm{SS}/\mathrm{df}$$

where B_k is the coordinate of the confidence region in the direction of the kth parameter (Draper and Smith 1981). This quadratic formula is difficult to solve for more than two parameters. To avoid this problem, we substituted the lower values of CI for B in Eq. 6 to calculate what joint confidence (α) region corresponded to that combination of individual confidence

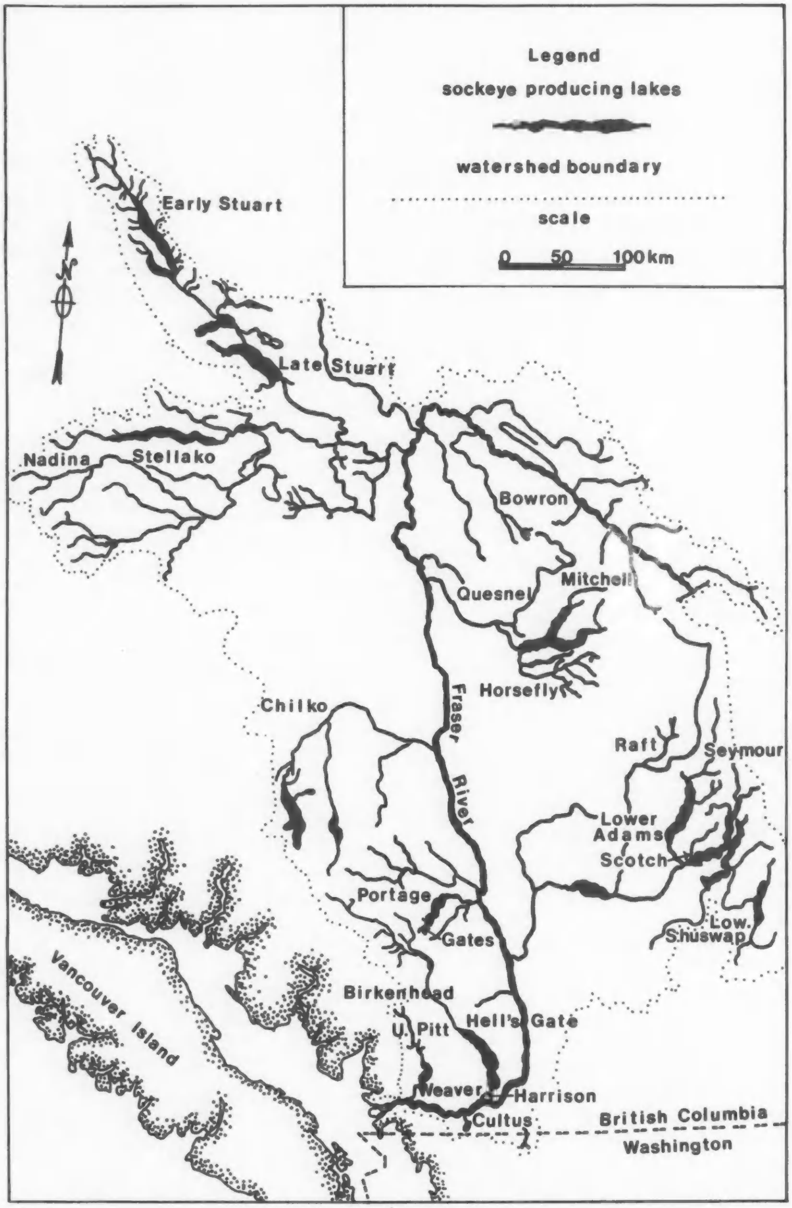
Legend
sockeye producing lakes
watershed boundary
scale
0 50 100km
Early Stuart
Late Stuart
Nadina
Stellako
Bowron
Mitchell
Quesnel
Horsefly
Chilko
Fraser River
Raft
Seymour
Lower Adams
Scotch
Portage
Gates
Low. Shuswap
Birkenhead
U. Pitt
Hell's Gate
Weaver
Harrison
Cultus
British Columbia
Washington
Vancouver Island
N

FIG. 1. Fraser River watershed showing the stocks of sockeye salmon and their nursery lakes.

intervals. Parameter sets identified in this manner were used as alternative stock–recruitment models that are consistent with the historical data.

Simulation Model

We built a simulation program to calculate the expected value of several harvest strategies for each alternative stock–recruitment model. The dynamics of the simulation model are basically the same as those assumed in fitting the regression model. Recruitment of the 10 stocks was simulated according to Eq. 1 with the regression parameter estimates. The program was initialized with escapement data up to 1985, the most recent year available. The mean age structure and sex ratio of returning adults were determined from historical data. Random errors were included as in Eq. 2 with variance–covariance matrix Ω. Thus the simulated errors are autocorrelated within stocks and cross-correlated among stocks with correlation coefficients estimated from the data.

The harvest policies consist of a harvest rate for each run-timing group and each simulated year. For each harvest policy and each alternative model, we simulated 100 random 40-yr projections, using the same random number sequence for each policy/model combination. The program calculated the median escapement and catch for each stock in each simulated year, the total Fraser sockeye catch each year, the cumulative 40-yr catch, and the corresponding coefficients of variation for each statistic.

Long-term yield is only one measure of the value of harvest policies. Also important is the extent to which experimental harvest policies make it possible to distinguish the potential causes of cyclic dominance. If there is no natural cause of cyclic dominance, as we assumed in the model, the off-year lines in cyclic populations should increase in abundance in response to lower harvest rates. The extent of this rebuilding can be measured by the ratio of successive escapements of the off-year lines. Escapement ratios are preferable to ratios of catch or total return because off-year lines are especially sensitive to errors in allocating catch among stocks. We chose the ratio of escapement after two generations (S_{t+8}) to current escapement (S_t) because DFO staff indicated that experimental plans would not be viewed favorably by industry or senior government officials unless they were likely to produce results within 8 yr. The normalized statistic, $\ln(S_{t+8}/S_t)$, is zero if there is no change in abundance and positive if there is rebuilding. The rebuilding index and its variance were calculated in the simulation program for each off-year line of the cyclic stocks. For each experimental design, we then calculated the probability of detecting a statistically significant response, should the off-years rebuild.

Harvest Policy Design

Fraser River sockeye salmon migrate through the commercial fishery from late June to late September (Woodey 1987). Migration is continuous but there are basically three run-timing groups that can be targeted at different harvest rates (Table 1). The early run-timing group is solely the Early Stuart stock, the mid-timing group includes the Early Miscellaneous, Quesnel, Late Stuart, Chilko, and Stellako stocks, and the late group comprises the Birkenhead, Shuswap, Weaver, and Late Miscellaneous stocks. With a 4-yr abundance cycle for each of three run-timing groups, there are 12 "windows" that can be assigned different harvest rates (Table 1). Even if we consider only six different levels of harvest, there are $6^{12} \approx 1$ billion different experimental designs to consider. Formal optimization methods could be used to find the best design by combining multiple performance criteria (e.g. long-term catch, lost fishing time, effects on other species) into a single objective function (Keeney and Raiffa 1976). In practice, different user groups would disagree about the weights assigned to different criteria and a more ad hoc approach is necessary.

We limited the number of harvest rate combinations to be tested by recognizing constraints imposed by the current cyclic abundance patterns and mixed-stock fisheries. We contend that the main focus should be on currently depressed off-year lines. It is unlikely that substantial increases in yield can be obtained by tampering with dominant lines that are already very abundant. Further enhancement of dominant lines would exaggerate the cyclic variation that already makes the fishery economically difficult to manage. If a focus on depressed lines is accepted, four of the cycle year/timing windows are off limits to extreme harvest-rate reduction: 1989E, 1988M, 1989M, and 1986L (notation is spawning cycle year and timing window: E, early; M, mid; L, late). Stellako is dominant in 1987M but its cycles are less pronounced that those of the other cyclic stocks.

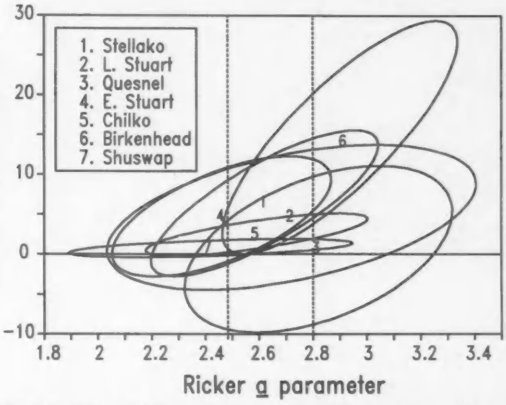

FIG. 2. Joint 95% confidence regions of the Ricker stock–recruitment parameters (Eq. 1) of seven major Fraser River sockeye stocks. The b parameter is in units of millions of spawners^{-1}. The confidence ellipses result from separate fits for each stock to data from brood years 1948–79. The number at the center of each ellipse indicates the location of the a and b estimates for each stock. The vertical broken lines indicate the 95% confidence limits of the common a value estimated from pooled regression with data on 10 stocks from brood years 1948–81.

A second criterion that further restricts the number of combinations to investigate is that extreme harvest-rate reductions should be applied to only one timing window each year, to minimize foregone catch and perhaps balance low harvest rates with higher harvest rates in another run-timing window. Under this criterion, good candidates for experimental harvest rate reductions are 1986E, 1987M, and 1988L. Early Stuart is an obvious choice because there is no conflict with other stocks. The 1988L Shuswap off-year is a better candidate for rebuilding than 1989L because of the conflict with pink salmon (*Oncorhynchus gorbuscha*) in 1989. In the 1987M window there is a conflict between trying to reduce harvest rates on the Quesnel and Late Stuart off-years and maintaining catches in what is the second lowest year in the cycle of total Fraser River catch. In the 1989 cycle year there is no good candidate for extreme harvest-rate reduction because the 1989E and 1989M windows contain dominant lines and in 1989L there is a conflict with odd-year pink salmon.

Results

We fit an aggregated (H_0) and disaggregated (H_1) form of the stock–recruitment model (Eq. 2). The stock-specific a estimates of the disaggregated model had overlapping confidence intervals (Fig. 2). The F statistic for the difference in sum of squares between the aggregated and disaggregated models (Eq. 4) was not significant ($F = 0.84$, $p > 0.25$). For the purposes of this paper we therefore accepted the null hypothesis of a common a parameter for all stocks.

Generalized weighted regression (Eq. 3) was used to correct the stock–recruitment parameter estimates for correlated residuals. Compared with the unweighted regression estimate, the common a value was unchanged by the weighted regression, but some of the b values did change. The first-order autocorrelation coefficients (ρ_i, Table 3) were mostly positive but none were significantly different from zero (all $p > 0.05$).

TABLE 3. Harvest rates (%) for maximum sustainable yield at equilibrium for each alternative model with the *a* parameter shown in the first row. The parameter ρ_i is the first-order autocorrelation coefficient of the residuals e_{it} from Eq. 2.

Stock	Model			
	Weak d.d.	Best fit	Strong d.d	p
Common *a*	2.49	2.63	2.77	
Early Stuart	67.6	70.1	73.9	0.206
Early Misc.	66.3	68.7	72.6	0.180
Quesnel	63.5	67.3	70.7	−0.157
Late Stuart	65.9	69.5	72.7	0.163
Chilko	68.4	71.7	74.8	0.169
Stellako	67.3	70.4	72.9	−0.233
Birkenhead	68.7	72.5	74.6	0.312
Shuswap	70.9	73.9	76.6	0.210
Weaver	69.8	73.5	72.7	0.281
Late Misc.	70.0	72.6	76.9	0.102

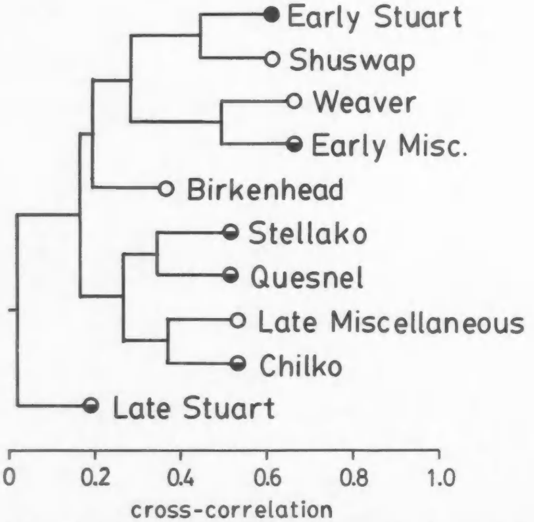

FIG. 3. Similarity of residuals (e_{it}) from the pooled stock–recruitment regression (Eq. 2). Cluster analysis, with group-average sorting, was performed on the correlation matrix of residuals. Run-timing groups: ●, early; ◑, midtiming; ○, late timing.

The cross-correlation coefficients of residuals among stocks were also mostly positive and ranged from −0.26 to 0.50. Cluster analysis of the cross-correlation coefficients (Fig. 3) reveals pairs of correlated stocks but not strongly correlated higher order groups, except for a weak clustering of some midtiming upper Fraser stocks (Stellako, Quesnel, and Chilko). The extent to which stocks respond similarly to environmental or other factors, as measured by the correlation of residuals, is important in designing managment experiments (Walters et al. 1988). In general, highly correlated stocks are good treatment–control pairs as long as the treatment is applied to one stock in each pair. However, if a treated group of stocks were not highly correlated with the control group of stocks, prior to treatment, the response to treatment would be more likely to be confounded with some extraneous factor.

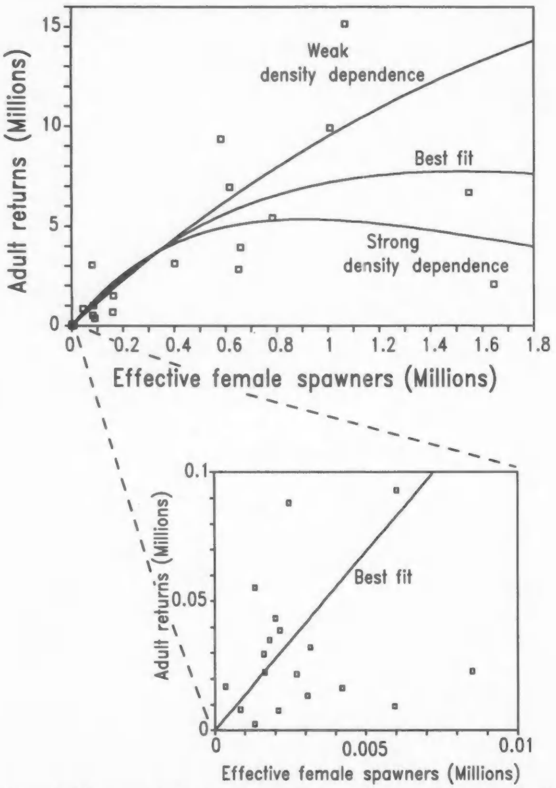

FIG. 4. Shuswap stock–recruitment data and three alternative fitted curves. The weak and strong d.d. curves correspond to 90% confidence intervals of the parameters, not of the best-fit curve. Data from the off-years are in the expanded insert.

The regression estimates of escapement for maximum recruitment (1/*b*, Table 2) are closely related to estimates based on independent stream surveys of spawning habitat capacity (Ian Williams, Pacific Biological Station, Nanaimo, B.C., pers. comm.). The parameter estimates and/or confidence intervals of three stocks were unrealistic. The dominant line of the Quesnel stock is increasing, apparently exponentially. The regression estimate of *b* was negative, which means the optimum escapement is undefined. For the Quesnel stock only, we used the stream survey index as a best estimate of 1/*b* and an estimate of lake capacity for the upper bound of 1/*b*. The *b* estimate for the Lake Stuart stock is positive, but the confidence interval intersected *b* = 0. For Weaver Creek the confidence interval on *b* is extremely wide because of additional variation in recruitment introduced by the spawning channel. Very low levels of *b* would correspond to escapements well beyond the spawning channel capacity. For both these stocks we again used the lake capacity estimate as the upper bound of 1/*b*.

The confidence interval of the common *a* parameter (Table 2) is much narrower than the confidence regions of the individual *a* parameters in the disaggregated fit (Fig. 2) because more data are used to estimate the common parameter. We used the individual 90% confidence intervals of the parameters to approximate the joint confidence region. Substitution of the lower 90% confidence intervals for *B* in Eq. 6 gave an *F* value corresponding to the joint 95% confidence region. The alternatives to the best-fit parameter set in Table 2 are thus extreme

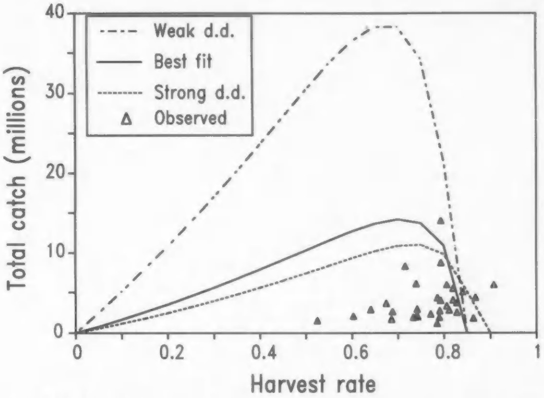

FIG. 5. Total yields of Fraser River sockeye salmon. The curves denote equilibrium catches predicted by three alternative models at a given harvest rate applied to all stocks. The triangles are total catches from 1954 to 1984 and corresponding harvest rates calculated as (total catch)/(total adult return).

parameter combinations that are still consistent with historical data.

We used the upper 90%, lower 90%, and best-fit parameter sets as alternative models to predict future recruitments. The *a* values of the models are not very different (Table 2); the big difference is the b_i values and thus the strength of density-dependent regulation. The lower parameter set has weak density dependence (small b_i) and therefore predicts the most optimistic recruitments at high stock size (e.g. Fig. 4). The upper parameter set has strong density dependence (large b_i) and thus predicts a more dome-shaped stock–recruitment curve. We hereafter refer to the three alternative models as weak density dependence (d.d.), best fit, and strong d.d.

The initial slope (determined by *a*) of the stock–recruitment curves (e.g. Fig. 4) is well determined but recruitment at high stock sizes (determined by *b*) is very uncertain. The harvest rate for maximum sustainable yield depends only on the initial slope (Ricker 1975) and thus differs little among models (Table 3). Slight differences in optimal harvest rate among stocks for the same *a* value result from stock-specific differences in sex ratio.

Very different total equilibrium yields are predicted by the different stock–recruitment models (Fig. 5). Even the strong d.d. model predicts higher yields than those obtained in the recent past. Predicted and observed harvest rates in Fig. 5 are not directly comparable because in the predicted case the same harvest rate is applied to each stock, while the observed total harvest rate is a weighted mean of observed harvest rates across stocks. Also, the actual stocks are not in equilibrium as defined by the Ricker model. Historically, lower harvest rates were obtained for some stocks in some years but these rates were not sustained long enough to compare observed yields against the Ricker model predictions.

Although the three alternative models predict different equilibrium yields, the optimum yields are obtained at similar harvest rates (Fig. 5). Thus, if the fishery were managed with a harvest-rate policy, there would be almost no additional present value in knowing which model is correct. Irrespective of which model is correct, target optimal harvest rates should be in the range 65–75% and not the 75 – 85% rates obtained in the past. Presently, the fishery is managed with an escapement policy, but optimum escapement levels are very uncertain (Table 2). If harvest rates are reduced to about 70% for several generations, the stocks should rebuild to a level determined by the strength of density-dependent interactions. Additional data at high stock sizes should then be sufficient to distinguish among alternative levels of density dependence.

Opportunities for Experimentation

There may be additional value in accelerating the rebuilding of some off-year lines by lowering the harvest rates beyond the 65 – 75% range that appears optimal in the long term. Accelerated rebuilding would give results sooner as to whether rebuilding will be successful, and if successful would give higher yields sooner than harvesting at the optimal equilibrium harvest rate. Using an in-season managment simulation model, K. McGivney (DFO, Vancouver, B.C., pers. comm.) found that a 50% harvest rate was the minimum level that could be achieved while still maintaining the number of fishing days within the range of recent season durations.

There are basically three run-timing groups that can be fished at different exploitation rates (Table 1). We confirmed the existence of these run-timing groups by performing a cluster analysis of stock-specific harvest rates realized from 1953 to 1984. The stocks clustered exactly as expected, with Birkenhead between the mid- and late groups as expected from its migration date (Woodey 1987).

Based on a wider set of preliminary simulation trials, four feasible harvest policies were identified by members of the Fraser River Task Force (FRTF), DFO's Cyclic Dominance Working Group, and the authors. Ranked in increasing degree of experimentation, the policies are (1) the FRTF baseline policy, which is somewhat depensatory and essentially maintains the status quo harvest rates that average about 80%; (2) the FRTF-recommended harvest rates, which are in the 65 – 75% range with 50 – 60% rates in 1986E; (3) the FRTF-recommended rates plus experimental rebuilding in the 1988L window; and (4) the FRTF-recommended rates plus experimental rebuilding in the 1986E, 1987M, and 1988L windows. The FRTF rates were derived from escapement targets that have been discussed by the FRTF (K. McGivney, pers. comm.) but they are not official recommendations of the FRTF. Experimental rebuilding of a given line means applying a 50% harvest rate for four generations and a 70% harvest rate thereafter. The policies are hereafter referred to as (1) baseline, (2) recommended, (3) late experiment, and (4) combined experiment.

The FRTF-recommended harvest rates are very close to the long-term optimal rates (Table 3) we estimated from the stock–recruitment data. The 1986E experimental rebuilding would be the easiest to achieve, but results from the Early Stuart alone may not be generalizable to other cyclic stocks. Harvest-rate reductions in 1988L would be the most definitive test of alternative explanations of cyclic dominance because the Shuswap stock has the most pronounced cycles. Reductions in 1987M would be very informative because two off-year lines (Quesnel and Late Stuart) would be affected, but would also be the most difficult to implement. Years and run-timing windows for harvest-rate reduction were also chosen to complement enhancement projects planned by the Salmonid Enhancement Program, especially fertilization of Chilko and Quesnel lakes. The combined experimental design would permit a 2 × 2 factorial com-

TABLE 4. Cumulative 40-yr catches (in millions of fish) of Fraser River sockeye salmon as predicted by alternative parameterizations of the Ricker model. The FRTF baseline is equivalent to a status quo policy. The late rebuilding experiment applies a 50% harvest rate to the late-timing 1988 lines for four generations. The combined experiment applies a 50% harvest rate to the early 1986, mid-1987, and late 1988 lines for four generations. All catches are geometric means of 100 Monte Carlo trials with random errors autocorrelated within stocks and cross-correlated among stocks. Values in parentheses are the coefficients of variation in mean catch.

	Model		
Harvest Policy	Weak d.d	Best fit	Strong d.d
FRTF baseline	**380** (36.0%)	**231** (24.7%)	**209** (21.1%)
FRTF recommended	**644** (21.7%)	**303** (16.2%)	**246** (14.5%)
FRTF recommended and late 1988 rebuilding	**685** (21.2%)	**313** (15.6%)	**251** (13.9%)
FRTF recommended, early 1986, mid-1987, and late 1988 rebuilding	**693** (21.7%)	**320** (15.7%)	**257** (13.8%)

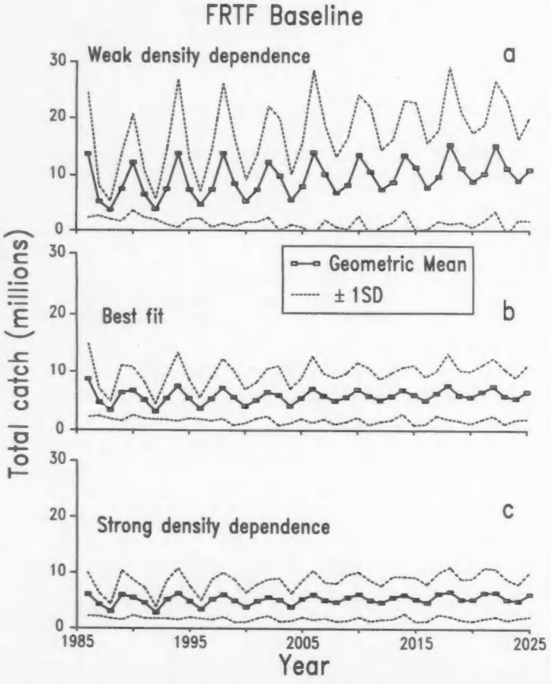

FIG. 6. Total Fraser sockeye catch simulated with FRTF baseline harvest policy and three alternative models. Solid lines are geometric means of 100 Monte Carlo simulations; broken lines are ± 1 SD.

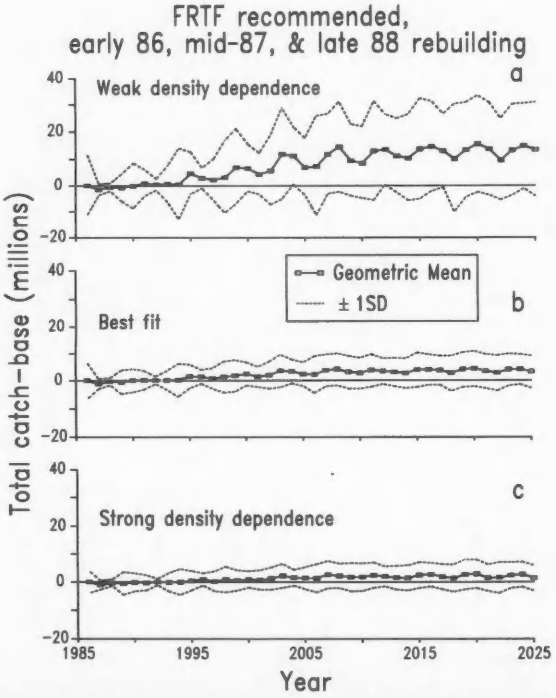

FIG. 7. Total Fraser sockeye catch simulated as in Fig. 6 except with the combined experimental policy, which includes the FRTF-recommended policy and accelerated rebuilding of the early 1986, mid-1987, and late 1988 lines. Each subplot is the difference between catch under the experimental policy and baseline catch for the same model.

parison of the effects of fertilization and harvest-rate reduction on recruitment of the off-year lines.

Simulation Model Results

The four harvest policies were evaluated with respect to expected 40-yr yields, foregone catch in the first 4-yr cycle, and the ability to detect rebuilding of the off-year lines after two cycles. Large increases in simulated yield resulted from the FRTF-recomended policy compared with the FRTF baseline (Table 4). Additional, but smaller increases resulted from the experimental rebuilding policies. The ranking of the policies was the same for all three models because the models mainly differ in the degree of density dependence. With weak density dependence, increases in yield above those from the baseline were tremendous for all harvest policies; with strong density dependence, increases were more modest. Yields predicted by the strong d.d. model were very close to those obtained with the Larkin model, except that the Larkin model predicted a lower baseline yield. Thus the values in Table 4 probably bracket the range of reasonable outcomes.

With the best-fit model and baseline harvest rates the cyclic pattern of catches gradually dampens out to an average annual

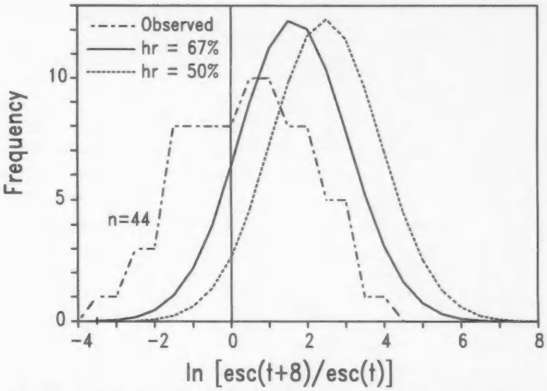

FIG. 8. Frequency of the ratio of escapements two generations apart for off-year lines of Fraser sockeye, for the historically observed case and two constant harvest rates (hr). The off-year lines included are Early Stuart (1986, 1987), Late Stuart and Quesnel (1987, 1988), and Shuswap (1988, 1989).

yield of about 5 million fish (Fig. 6b), a value within the range of historical total catches (Fig. 5). With the weak d.d. model, the cyclic pattern is maintained longer and yield increases even under the baseline policy (Fig. 6a). Such large yields under the baseline seem unlikely given the wide confidence intervals and the fact that a total yield greater than 10 million occurred only once in the past 35 yr (1958).

Expected rebuilding trajectories under the FRTF recommended and late experimental policies are not shown but were quite similar to those of the combined experiment (Fig. 7). Foregone catch is defined as a negative difference in catch between the rebuilding policies and the baseline. Cumulative foregone catch ranged from 2 to 3 million fish and in almost all model/policy cases was confined to the first 4-yr cycle (Fig. 7). With the best-fit model and the combined experimental rebuilding policy, an additional 3 – 4 million fish per year would be available to the fishery after 20 yr, compared with the baseline policy (Fig. 7b). The expected increase over baseline catches is itself cyclic because the biggest gains are expected in the 1988 lines, which are currently the smallest in the 4-yr cycle.

Rebuilding of the off-year lines can easily be estimated with Eq. 1 because the density-dependent term (bS_t) would be negligible for the first few generations. With no harvesting of the off-year lines, 50-fold increases in escapement would be expected in two generations. Even at the minimum attainable harvest rate of 50%, the off-year lines should increase 10-fold in two cycles. Actual rebuilding rates will also be affected by natural variability, making it more difficult to discern the effect of reduced harvest rates. We examined this variability by calculating the ratio of off-year escapements two generations apart. The frequency distribution of these ratios was approximately normal when log transformed (Fig. 8). The mean of the historically observed escapement ratio distribution is slightly greater than zero (0.15). The constant harvest rate which would produce this mean is 84%, a value slightly greater than the mean 80% harvest rate those off-year lines actually experienced. The standard deviation of this distribution (1.54) is only slightly greater than the expected standard deviation due to natural variability alone (1.41) as estimated from the regression residuals. Also shown in Fig. 8 are expected distributions of escapement ratios calculated for harvest rates of 67%, in the range recommended by the FRTF, and 50%, attainable with experimental rebuilding.

The mean and variance of escapement ratios were also calculated by the stochastic simulation model. After two cycles, the number of observations is simply eight, the number of off-year lines. Even with the baseline harvest rates there is some rebuilding of the off-years (Fig. 6) which is inconsistent with the historical response of the off-years to high harvest rates. As discussed below, the Ricker model with harvest-rate management is unable to exactly recreate the cyclic patterns observed in the past. We therefore subtracted the mean baseline escapement ratio from the escapement ratios expected after two generations with the three rebuilding policies. We then calculated statistical power (Dixon and Massey 1969), the ability to correctly detect an increase in abundance of the off-year lines compared with abundance in the baseline case, assuming a one-tailed t statistic and $\alpha = 0.05$. The probability of detecting a response, should the off-years rebuild, was 0.4 for the FRTF-recommended policy, 0.58 for the late experiment, and 0.66 for the combined experiment. Therefore, some experimentation, beyond the FRTF recommendations, is required to give more than a 50% chance of correctly detecting a response after two generations.

Discussion

We began this work with the notion that the large number of Fraser River sockeye salmon stocks would provide an ideal case for experimental management. However, the severe constraints caused by the overlap in run timing of many stocks with quite different abundances forced a reduction in the complexity of the experimental design. We suspect that this situation may characterize many other multistock and multispecies fisheries. The challenge, therefore, is to develop the most informative and productive management plans within these constraints.

We have identified several harvest policies that, if implemented, could significantly increase the yield of one of Canada's most valuable fisheries. The advantage of formulating policy by workshop consensus, rather than formal optimization techniques, is that one of the three rebuilding plans is likely to be implemented. While rebuilding strategies for Fraser River sockeye are being evaluated, some rebuilding through harvest-rate reduction is already occurring. Benefitting from reduced harvest rates, the 1988 Early Stuart line has increased 30-fold in five generations. The 1987 escapement of the subdominant Shuswap line was the highest in 20 yr; in the past, this line was deliberately suppressed. The success of this limited rebuilding encourages further experimentation. The current question is, should harvest rates be lowered in all year/timing windows and are more extreme reductions in some windows justified?.

Harvest-rate reductions would test one hypothesis about the causes and maintenance of cyclic dominance: the role of harvesting. If depensatory fishing were the sole cause of cyclic dominance, reduced harvest rates should increase yields dramatically (Table 4). If there is a biological explanation of cyclic dominance, the optimal fishing policy is unclear. There are actually two subhypotheses about biological causes of cyclic dominance: (a) the off-years are kept at low abundance by depensatory predation and (b) the existence of large subdominant runs would suppress the dominant lines through brood-year interactions. If only the first part of the hypothesis is true, a general reduction of harvest rates may still be worthwhile. If subdominant suppression also exists, depensatory fishing may (but not necessarily, Collie and Walters 1987) be optimal.

If there is a biological explanation of cyclic dominance, experiments in addition to harvest-rate reduction, such as fertilization and/or predator removal, would be required to elucidate the mechanism. Of possible experiments, harvest-rate reduction should be given top priority because it is the factor of primary management importance. From a management perspective, understanding the mechanism of cyclic dominance may not be necessary unless management action based on that mechanism is contemplated.

As noted above, the simulated Ricker model did not maintain cyclic dominance when harvested with the baseline policy. The baseline harvest rates are similar to historical harvest rates *on average*, but in the past, some off-year lines sustained >90% exploitation, which reinforced the cycles. Even when the simulated populations were subject to historical harvest rates, some rebuilding of the off-year lines occurred. This inadequacy may result from shortcomings of the population dynamics model and/or the simulated harvest-rate management. The fishery is actually managed with an escapement policy which makes it easier to deliberately induce cycles. There is no credible model for biological maintenance of cyclic dominance; more complicated depensatory models can be proposed in theory, but the parameters of such models are not well defined with existing data. The proposed rebuilding strategies should result in more informative data with which to test depensatory models.

Pooled regression is an excellent way to extract mean relationships from highly variable data on a number of stocks. This method gave a more precise estimate of the Ricker *a* value than did stock-specific regressions because a large number of data were pooled to estimate the mean productivity of sockeye salmon. There may be stock-specific differences in productivity but the common *a* assumption gave the best predictive model with existing data. A pooled regression approach was used by Anderson and Wilen (1985) to estimate the effects of stock size and environmental factors on three populations of coho salmon. They also concluded that a pooled *a* parameter was appropriate, which allowed more degrees of freedom to estimate environmental effects. Reisenblichler (1987) noted a similarity in Ricker *a* values estimated for chinook salmon (*Oncorhynchus tschawytscha*) from British Columbia to northern California and suggested that a pooled productivity estimate could be used to set harvest rates for stocks with unknown stock–recruitment relationships.

Stocks exploited together cannot be managed for stock-specific escapement goals. Fraser sockeye have been managed by setting escapement targets for one stock (usually dominant) in each run-timing window. Catch of the dominant lines is thus optimized at the expense of the off-year lines. If the unexplained variability in recruitment is highly correlated among stocks in a mixed fishery, a fixed escapement policy is optimal; if the residual variation is uncorrelated, a fixed harvest rate is best (Hilborn 1985). In the case of Fraser River sockeye, the residuals from the stock–recruitment model are not highly correlated among stocks within each run-timing group (Fig. 3), and therefore a fixed harvest rate policy is optimal.

Our simulated management policy applied a common harvest rate to each run-timing group. In theory, the optimal harvest rate in a mixed-stock fishery depends on the run size of each stock relative to its equilibrium (Hilborn 1976). Stochastic dynamic programming can be used to calculate the best harvest rate for all combinations of constituent stock sizes. In the case with equal *a* and unequal *b* parameters, the best common harvest rate was quite insensitive to relative stock size (Hilborn 1976).

Dynamic programming has also been used to investigate the value of deliberate experiments to distinguish alternative recruitment hypotheses (Walters 1981). In the situation with *a* known and *b* highly uncertain, the expected value of the actively adaptive policy was only slightly higher (0.1 – 0.5%) than the value of the passive adaptive policy. We reached a similar conclusion in the present study: the value of learning which model is correct was only 0.26% greater than the value of applying what appears to be the optimal harvest rate now. In theory, dynamic programming could be used to calculate optimal harvest rates of Fraser River sockeye, but in practice the combination of 10 stocks and several alternative models would cause severe numerical problems. However, the qualitative results of simpler dynamic programming calculations can still be used to guide policy formulation.

The present study was intended to investigate the long-term value of rebuilding strategies, and not to stimulate within-season management of sockeye salmon. Large increases in simulated catch resulted from applying the FRTF-recommended harvest rates and more modest increases from experimentally rebuilding the off-years. Cumulative yields reported in Table 4 were calculated without discounting. The ranking of the four harvest policies was unchanged when cumulative yields were calculated with the 10% discount rate mandated for Canadian government projects. A large increase still occurred with the FRTF-recommended policy, but the value of the two experimental options was virtually identical. Obviously, experimentation is less valuable if future yields are highly discounted.

Enhancement methods could potentially ease foregone catches during the first few generations of rebuilding, especially in the 1987M window. Portable incubation facilities have been used to give small off-year runs a head start (Williams 1987). Planned spawning channels could provide new habitat for up to 10^5 spawners, but could not compensate the immediate foregone catch because the facilities are not yet operational. Delaying rebuilding until enhancement facilities are operational would also mean delaying expected benefits. Enhancement is not a substitute for harvest-rate reduction because the potential benefits of reduced harvest rates are at least an order of magnitude greater than those from enhancement projects planned in the Fraser River watershed.

In conclusion, the modeling approach used here is useful for predicting the mean response of populations to various harvest strategies. Recommended harvest rates in the range 60 – 70% should result in large increases in yield regardless of which population model is correct. Thus the FRTF-recommended policy appears to be robust to uncertainty about the population dynamics. More deliberate experimentation is necessary to test whether the off-years will rebuild in response to reduced exploitation. The late 1988 experimental rebuilding policy is a good compromise between the need for information from important stocks (such as Shuswap) and pressure to keep the fishery open.

Acknowledgments

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Effects of Large-Scale Metalimnetic Migration Events on Phosphorus Dynamics in a North-Temperate Reservoir

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In Eau Galle Reservoir, Wisconsin, early in the stratified period of 1982, hypolimnetic anoxia developed, soluble reactive phosphorus concentrations increased above the profundal sediment surface, and internal total phosphorus loading was high. Shortly thereafter, the passage of a cold front with high wind power resulted in mixing and a pronounced descent of the metalimnion. During this event, previously anoxic water within the metalimnion and upper hypolimnion became reoxygenated, internal total phosphorus loading declined to a minimum, and a loss of total phosphorus mass occurred from the metalimnion and hypolimnion. Total phosphorus mass in the epilimnion remained constant during this period. A similar pattern occurred during a large, wind-driven migration of the metalimnion in early August. During such events, phosphorus sedimentation rates increased in the hypolimnion, reflecting the loss of total phosphorus mass from the water column. In contrast, other investigations of lakes have reported that phosphorus is entrained into the epilimnion during metalimnetic migrations, rather than lost through sedimentation. Phosphorus sedimentation during large metalimnetic migration events in Eau Galle Reservoir may occur because previously anoxic water containing iron becomes reoxygenated, causing the coprecipitation and sedimentation of oxidized iron and phosphorus.

Au début de la période de stratification de 1982 dans le réservoir Eau Galle (État du Wisconsin), on a noté la présence d'une anoxie hypolimnique, d'une augmentation des concentrations de phosphore réactif soluble à la surface des sédiments profonds et d'un niveau élevé de la charge interne de phosphore total. Peu après, le passage d'un front froid accompagné de vents violents a entraîné le brassage des eaux et l'enfoncement marqué du métalimnion. Les eaux auparavant anoxiques du métalimnion et de la partie supérieure de l'hypolimnion ont ainsi été réoxygénées et la charge interne de phosphore total a baissé à son minimum tandis que le métalimnion et l'hypolimnion ont subit une perte de masse totale de phosphore. Par contre, la masse totale de phosphore dans l'épilimnion est demeurée constante pendant cette période. On a aussi noté un tel régime pendant une grande migration du métalimnion au début d'août entraînée par des vents. À de telles occasions, les taux de sédimentation du phosphore augmentent dans l'hypolimnion; ceci traduit une perte de la masse totale de phosphore dans la colonne d'eau. Par contre, d'autres chercheurs ont signalés que le phosphore est entraîné dans l'épilimnion au cours de la migration métalimnétique et non perdu par sédimentation. La sédimentation du phosphore au cours d'importantes migrations métalimnétiques dans le réservoir Eau Galle peut être causée par la réoxygénation de l'eau auparavant anoxique et contenant du fer, ce qui entraîne la coprécipitation et la sédimentation du fer oxydé et du phosphore.

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Lakes experiencing hypolimnetic anoxia during stratification often exhibit marked increases in phosphorus (P) concentrations that cannot be accounted for by external P loading. Concentrations of P usually increase with increasing depth in the hypolimnion, a pattern closely related to depthwise changes in the area to volume ratio and the progression of anoxia (Stauffer 1985). An increasing body of evidence indicates that anoxic, profundal sediments are an important source of internal P loading and contribute significantly to patterns of increase in P mass in the hypolimnetic water column (Mortimer 1941; Cooke et al. 1977; Theis and McCabe 1978; Larson et al. 1981; Nurnberg 1984, 1987; Riley and Prepas 1984, Nurnberg et al. 1986). Disassociation of iron–phosphorus complexes under reduced conditions is one possible mechanism of sediment P release (Mortimer 1941, 1942).

P released from anoxic sediment may become an important source to the epilimnion via vertical transport mechanisms and have a regulatory effect on phytoplankton productivity when external P loading is minimal. P may be transported vertically into the epilimnion by turbulent eddy diffusion (Jassby and Powell 1975; Imboden and Emerson 1978; Robards and Ward 1978; Stefan and Hanson 1981; Wodka et al. 1983). In addition, wind-driven downward migrations of the metalimnion may result in the entrainment of metalimnetic and hypolimnetic P into the epilimnion. Several investigations have reported the occurrence of wind-induced metalimnetic migrations with accompanying increases in epilimnetic P and algal biomass (Stauffer and Lee 1973; Kortmann et al. 1982; Stauffer and Armstrong 1984; Stauffer 1985, 1987; Effler et al. 1986). Conversely, during periods of low wind power and stable stratification, little if any P may be transported upward (Gaugush 1984), particularly if P gradients are minimal in the metalimnion (Stauffer 1985). Thus, an understanding of internal P loading from anoxic, profundal sediments and potential transport to the surface waters is of importance to the P economy of the epilimnion.

Internal P loading from anoxic sediment and the effects of wind-induced metalimnetic migrations on P dynamics were examined in Eau Galle Reservoir, Wisconsin. Gaugush (1984) previously reported that during periods of declining stability in the summer, migrations of the metalimnion occurred in Eau Galle Reservoir as a result of high wind power. When little or no change in the heat content of the lake occurred, migrations were small, and increases in epilimnetic P followed, suggesting entrainment of P from deeper water or the metalimnetic shelf sediments (e.g. Stauffer and Armstrong 1984). However, passage of cold fronts that caused a decrease in the heat content of the lake resulted in large downward migrations of the metalimnion into previously anoxic water during wind-induced mixing. Gaugush (1984) found that these large metalimnetic migration events resulted in a loss of P from the water column, rather than entrainment of P into the epilimnion, which is contrary to those patterns observed in other lakes. Herein, we specifically examine P dynamics during these large metalimnetic migration events and propose possible mechanisms by which P loss from the water column may occur.

Methods

Study Site

Eau Galle Reservoir is a small (0.6 km^2) U.S. Army Corps of Engineers impoundment located in west-central Wisconsin. The reservoir is approximately circular in shape and has a mean depth of 3.2 m and maximum depth of 9.0 m. The reservoir receives the majority of its water input from the Eau Galle River (80–90%); other minor inflows are French, Lousey, and Lohn creeks. High inflows are usually confined to the fall and late winter months. Eau Galle River inflows are frequently <0.2 $m^3 \cdot s^{-1}$ during summer stratification. The outlet structure discharges from both surface and hypolimnetic ports. Surface discharge is uncontrolled and occurs at pool elevations above 286.5 m mean sea level. Discharge during the stratified period occurs primarily through a controlled vertical slide gate located 7.2 m below the reservoir's surface discharge.

Stratification and P Budget Determinations

Temperature and dissolved oxygen were determined at weekly intervals in Eau Galle Reservor with a Hydrolab Surveyor that was calibrated against Winkler dissolved oxygen determinations (APHA 1980). Measurements were collected at 1-m depth intervals from the surface to 0.5 m above the sediment surface in the deepest region of the lake. The upper and lower metalimnetic boundries in the reservoir were estimated by calculating the relative thermal resistance to mixing (RTRM) according to the equation RTRM = $(p_z - P_{z+1})/(p_{5°C} - p_{4°C})$ where p is the density of water at depth z (Vallentyne 1957). An RTRM of 30 was used to estimate these boundries (Kortmann et al. 1982; Gaugush 1984).

Eau Galle Reservoir, inflows, and the outflow were sampled biweekly from May until August 1982 for total phosphorus (TP), soluble reactive phosphorus (SRP), and total iron (TFe). Water samples were collected with a pump and hose in the deepest region of the reservoir at 1-m intervals from the surface to 0.5 m above the sediment surface. SRP was determined for samples filtered through 0.45-μm membrane filters. Samples from anoxic water were pumped from the hose directly into syringes to prevent air exposure and immediately pushed through a filter membrane. TP was digested by potassium persulfate oxidation (APHA 1980). TP and SRP analyses were performed on a Technicon Auto-Analyzer II using the automated ascorbic acid colorimetric method (APHA 1980). TFe was analyzed by atomic absorption spectrophometry following nitric acid digestion and reflux (APHA 1980).

Internal TP loading was calculated as the change in TP mass of the reservoir plus TP outputs minus TP inputs. TP mass was determined as the sum of volume-weighted TP mass of the water column. TP mass in the epilimnion, metalimnion, and hypolimnion (defined here on the basis of the location of the upper and lower metalimnetic boundries) was determined as the sum of volume-weighted TP mass within each density region. TP inputs and outputs were calculated as the product of the flow rate and the TP concentrations. Flow readings were obtained from continuous-recording gauges located on the Eau Galle River, the outflow, and the various streams (U.S. Geological Survey).

Sedimentation rates were measured at biweekly intervals with sedimentation traps suspended at the 4- and 8-m depths. Sedimentation trap cylinders had an aspect ratio of 3.0, which was low compared with other investigations (e.g. Lau 1979; Bloesch and Burns 1980) that recommend an aspect ratio of no less than 5.0 – 10.0 to prevent undertrapping in turbulent environments. Our sedimentation measurements may, therefore, be biased. A 5% salt solution was placed in each cylinder to minimize potential water movements and sediment resuspension within the cylinders. Samples obtained from three replicate cylinders at each depth were analyzed for TP on a Technicon Auto-Analyzer II after persulfate oxidation (APHA 1980). Sedimentation rates were calculated as the TP mass divided by the cylinder area and days of deployment.

Evaluation of SRP and DFe in the Metalimnion and Hypolimnion

A secondary investigation was conducted from May to July 1982 to examine SRP concentrations at close depth intervals and internal SRP loading in the reservoir. Internal SRP loading was calculated in the same manner as internal TP loading. Water samples, collected from the 8.95-m (i.e. 5 cm above the sediment surface) to the 4.6-m depth, were taken every 2 – 5 d in May and weekly to biweekly in June and July with a pneumatically operated close-interval sampler as described by Blakar (1979). The sampler consisted of a copper tubing manifold with ports located at 10-cm depth intervals. Attached to each port was a 50-mL plastic syringe with a plunger. A filter holder containing a 0.45-μm filter membrane was attached to the end of each syringe. A gauged pressure of 20 psi (137.9 kPa) was maintained in the sampler to prevent premature sampling in deep water. The sampler was attached to a pully-driven suspension system located in the deep, central region of the reservoir, carefully lowered, and left undisturbed for 2 h. The suspension system was designed to allow placement of the bottom

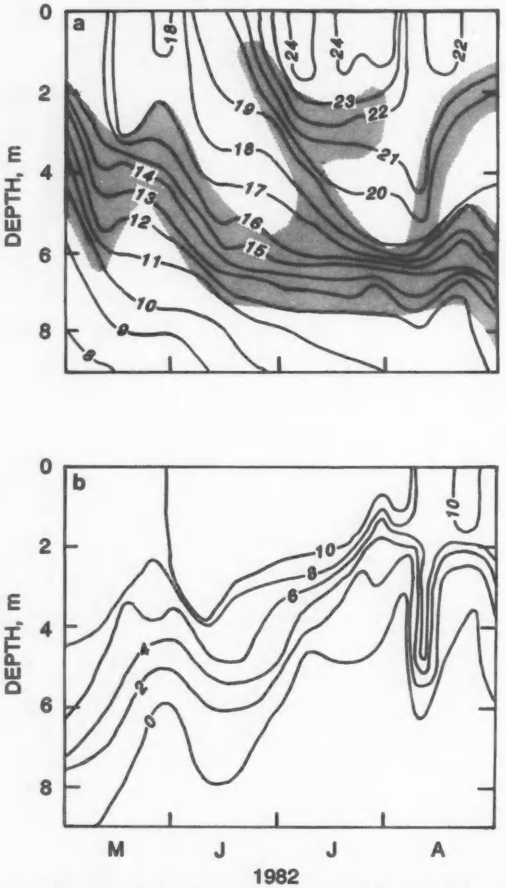

FIG. 1. Contour plot of (a) temperature (°C) and (b) dissolved oxygen (mg·L^{-1}) versus depth from May until August 1982. Shaded area represents the approximate location of the metalimnion estimated from RTRM = 30.

syringe to within 5 cm of the sediment surface. The pressure was released and a low vacuum was maintained in the sampler with a hand pump to collect in situ filtered samples for SRP. Samples for dissolved iron (DFe), analyzed by atomic absorption spectrophotometry after acidification to pH 1.0 with nitric acid (APHA 1980), were obtained from syringe samples collected within the bottom 1 m of the reservoir.

Results and Discussion

Stratification Dynamics

Following ice-out and vernal overturn in April 1982, the reservoir exhibited stratified conditions in early May (Fig. 1a). The metalimnion occurred between the 2- and 4.5-m depths in late May. Cold fronts followed by high wind power in early June and early August resulted in pronounced descents of the metalimnion. During these periods, the upper metalimnetic boundry moved from about the 2- to 5-m depth. Surface temperatures declined shortly before or during each large metalimnetic migration event.

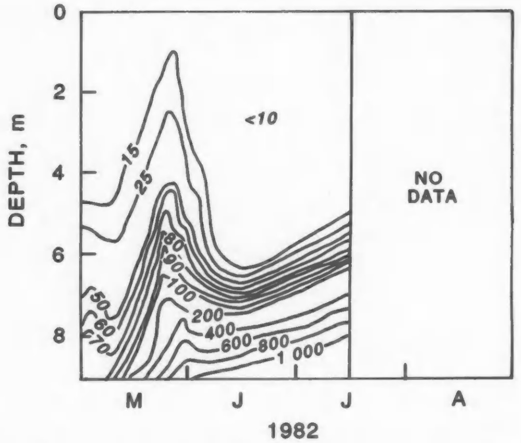

FIG. 2. Contour plot of close-interval (10 cm) changes in SRP (μg·L^{-1}) versus depth from May until July 1982.

Anoxic conditions occurred above the sediment–water interface (i.e. 0.5 m above the sediment surface) in early May and ascended to the 6-m depth in late May (Fig. 1b). During downward migration of the metalimnion in June, the depth of anoxia was restricted to 8 m and dissolved oxygen increases occurred between the 4- and 8-m depths. Anoxia ascended to the 3-m depth in late July. The large metalimnetic migration event in early August resulted in a deepening of the anoxic zone to 6 m and increases in dissolved oxygen between the 3- and 6-m depths.

Hypolimnetic SRP Dynamics at Close Depth Intervals

SRP began increasing above the sediment–water interface (i.e. 5 cm above the sediment surface) in early May (Fig. 2). In late May, SRP was elevated in the lower metalimnion and steep vertical SRP gradients were observed in the hypolimnion. Downward migration of the metalimnion in June resulted in a decrease in SRP in the metalimnion and upper hypolimnion. From mid-June until July, SRP gradients were confined primarily to the hypolimnion. SRP continued to increase above the sediment–water interface from June until mid-July.

Much of the hypolimnetic SRP appeared to originate from anoxic, profundal sediments (Fig. 3). Elevated SRP was observed above the sediment–water interface 5 d after anoxia was observed. SRP increased rapidly with depth and time during May, coinciding with the growth of the anoxic zone. A strong relationship was observed between SRP and DFe within the bottom 1 m of the hypolimnion (Fig. 4), after the establishment of anoxic conditions, suggesting that Fe–P disassociation was an important mechanism of sediment P release.

The extent of SRP accumulation was confined to the region near the lower metalimnetic boundry, and concentration gradients appeared to be influenced by hypolimnetic withdrawal (Fig. 3). SRP accumulation was observed between the reservoir bottom and the lower metalimnetic boundry in late May, when the hypolimnetic volume (52 000 m^3) and zone of anoxia were large (Fig. 3a). SRP accumulation through time was greatest between the 7- and 8.95-m depths, which occurred below the hypolimnetic withdrawal structure. The metalimnetic migration event in June resulted in a decrease in the hypolimnetic volume (17 000 m^3), the zone of anoxia, and SRP concentrations above

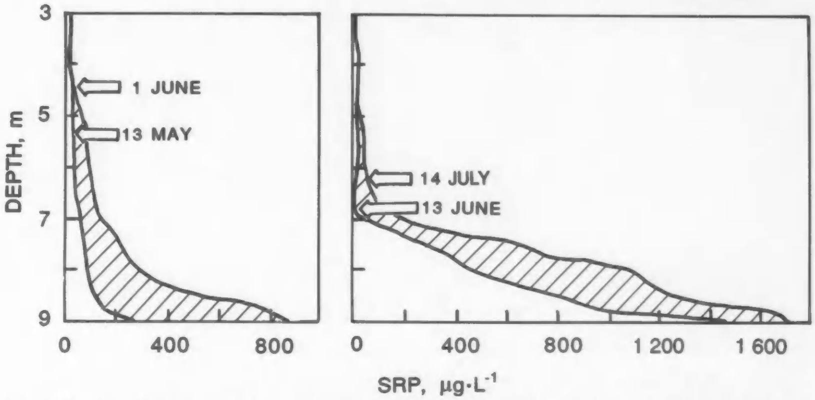

FIG. 3. Detailed changes in SRP versus depth, measured at 10-cm intervals, before and during the June metalimnetic migration event. Striped areas represent zones of SRP accumulation on successive dates. Arrows represent approximate location of the lower metalimnetic boundry.

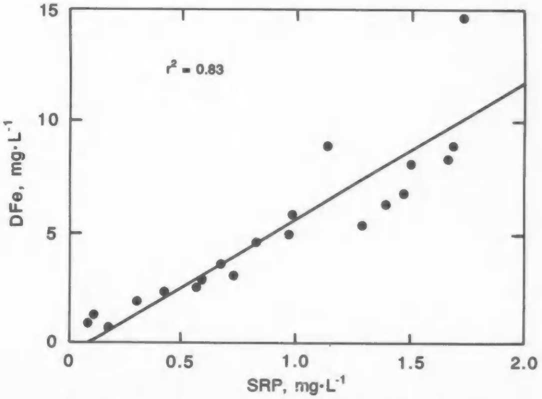

FIG. 4. Relationship between SRP and DFe within the bottom 1 m of the hypolimnion during anoxia.

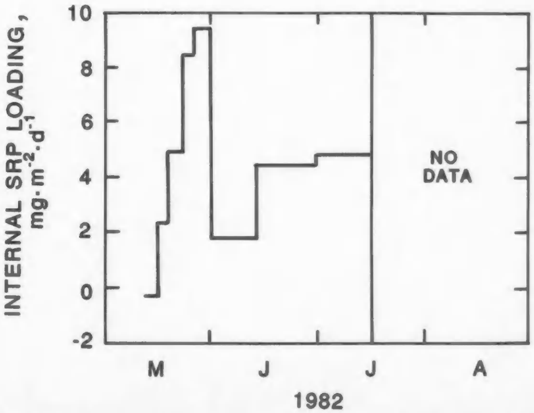

FIG. 5. Internal SRP loading determined by close-interval sampling from May to July 1982.

the 7-m depth (Fig. 3b). SRP increases above the 7-m depth. Increases in SRP concentration within the 5 to 7-m depth range in mid-July coincided with an increase in hypolimnetic volume and the zone of anoxia.

Internal SRP loading was influenced by the large metalimnetic migration event in June (Fig. 5). Internal SRP loading increased to a maximum in late May and then decreased to a minimum during the metalimnetic migration event. The rate increased in late June and July as the hypolimnetic volume and zone of anoxia increased.

TP Dynamics

Internal TP loading reached maxima in May, mid-July, and late August, during periods when wind power was low and the zone of anoxia was large (Fig. 6a). During these periods, external TP loading was low and constant at about 1 $mg \cdot m^{-2} \cdot d^{-1}$, accounting for less than 10% of the total (i.e. internal and external) TP loading to the reservoir. During periods of metalimnetic migration in June and early August, internal TP loading decreased to minima.

During periods of metalimnetic migration, epilimnetic TP mass either remained constant or showed net losses rather than net gains (Fig. 6b). Metalimnetic and hypolimnetic TP mass both decreased during the June metalimnetic migration event. During the early August migration event, TP mass decreased in the metalimnion and remained constant in the hypolimnion. These results indicated that during periods of large metalimnetic migration, (1) internal TP loading declined, (2) TP was not entrained into the epilimnion, and (3) a loss of TP mass occurred from the metalimnion and/or hypolimnion. Sedimentation of TP mass appeared to have been occurring during these events.

Since losses in TP mass occurred primarily in the metalimnion and hypolimnion, sedimentation rates determined between May and August were converted into hypolimnetic TP sedimentation rates (hypolimnetic TPsed rates) by subtracting values obtained at the 4-m depth from those measured at the 8-m depth (e.g. Kimmel and Goldman 1977; Hargrave and Taguchi 1978). Hypolimnetic TPsed rates exhibited maxima during large metalimnetic migration events (Fig. 7) and decreased to minima during periods when the metalimnion was stable. These results suggested that TP mass was lost from the water column through sedimentation during periods of metalimnetic migration.

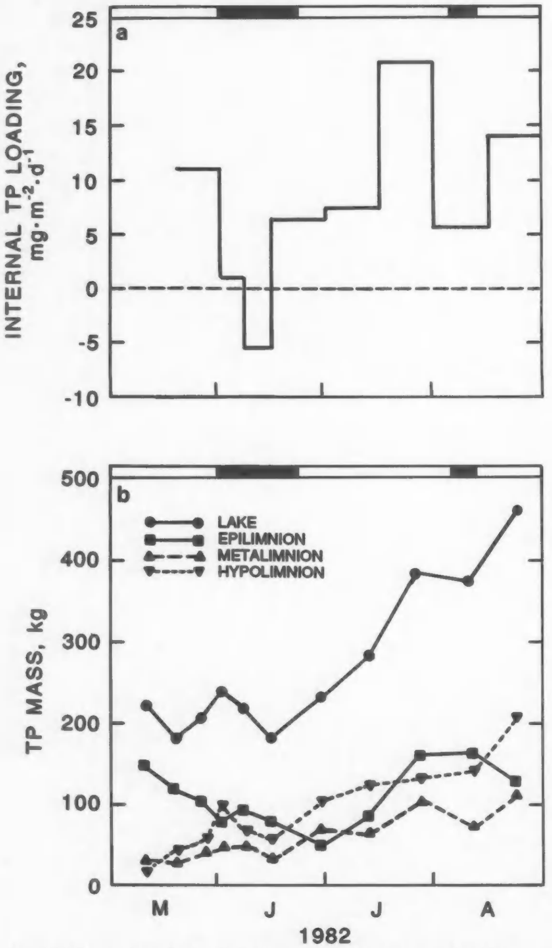

FIG. 6. Seasonal variations in (a) internal TP loading and (b) TP mass of the lake, epilimnion, metalimnion, and hypolimnion from May to August 1982. TP mass estimates of the epilimnion, metalimnion, and hypolimnion take into account changes in the volume of each density layer as a result of mixing. Blackened areas above figures represent periods of large, downward, metalimnetic migration.

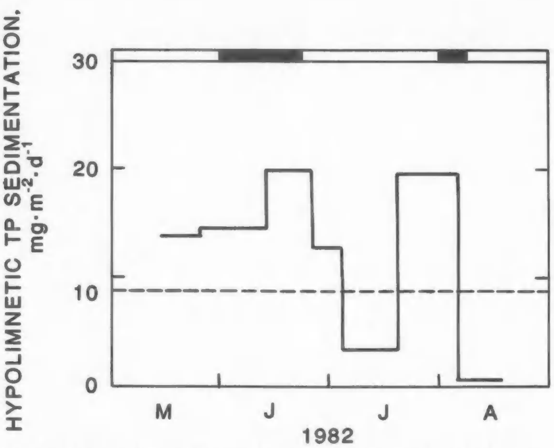

FIG. 7. Seasonal variations in hypolimnetic TP sedimentation rates from May until August 1982. Rates were calculated as the difference between sedimentation at 4 and 8 m. The broken line denotes the mean, baseline hypolimnetic TP sedimentation rate during periods when the metalimnion was stable. Measured rates occurring above this line represent hypolimnetic TP sedimentation gains, while those below the line represent hypolimnetic TP sedimentation losses. Blackened areas above the figure represent periods of large, downward, metalimnetic migration.

To compare hypolimnetic TPsed rates with TP mass losses from the water column during metalimnetic migration events, a correction factor was determined to account for depth-related differences between sedimentation rates at 4 and 8 m when the metalimnion was stable. The mean hypolimnetic TPsed rate during stable stratification (i.e. during late May, early July, and mid-August) was assumed to be a baseline hypolimnetic TPsed rate. Hypolimnetic TPsed rate gains or losses during the large metalimnetic migration events were calculated as the difference between the measured hypolimnetic TPsed rate and the mean, baseline hypolimnetic TPsed rate (Fig. 7). The surface area of the reservoir at the 4-m depth was used to convert hypolimnetic TPsed rate gains or losses to hypolimnetic TP mass gains or losses.

During the first migration event in June, the reservoir water column lost a net 50 kg of TP. Hypolimnetic TPsed rates, corrected for the baseline hypolimnetic TPsed rate, exhibited a net gain of 30 kg, accounting for 60% of the TP mass lost from the water column. During the second migration event in early August, the reservoir water column lost a net 5 kg of TP, while the hypolimnetic TPsed rate gain amounted to 20 kg. The larger value obtained from sedimentation traps may have been the result of sediment resuspension and transport of additional TP from the sides of the reservoir basin.

The reasons for sedimentation of TP mass during metalimnetic migration events are probably complex. Expansion of the epilimnion may move phytoplankton to depths where light penetration is low, thereby promoting death and settling. Barko et al. (1984) and Gaugush (1984) observed decreases in phytoplankton biomass and shifts in species composition during large metalimnetic migrations in Eau Galle Reservoir.

Reoxygenation of previously anoxic water may have caused the oxidation of Fe and adsorption of P. During periods of low wind power, the anoxic zone increased and the accumulation of TP and TFe occurred in the metalimnion or upper hypolimnion of Eau Galle Reservoir (Fig. 8). Large metalimnetic migration events caused a decrease in the anoxic zone and concomitant reductions in TP and TFe concentrations in reoxygenated areas of the metalimnion and upper hypolimnion. Davison et al. (1980, 1982) indicated that Fe transformations from reduced to oxidized states are very dynamic at the oxic–anoxic interface. Oxidation of Fe, adsorption of P onto these complexes, and sedimentation may be an important mechanism explaining the loss of TP mass from the water column during large metalimnetic migration events.

Results from this investigation differ from others that have observed entrainment of P into the epilimnion during metalimnetic migrations. Stauffer and Armstrong (1984) suggested that P entrainment into the epilimnion during migration events occurs when the anoxic zone includes a portion of the metalimnetic shelf sediments. However, reduced Fe in the anoxic metalimnion may become oxidized if oxygen is reintroduced during metalimnetic migration events, resulting in adsorption

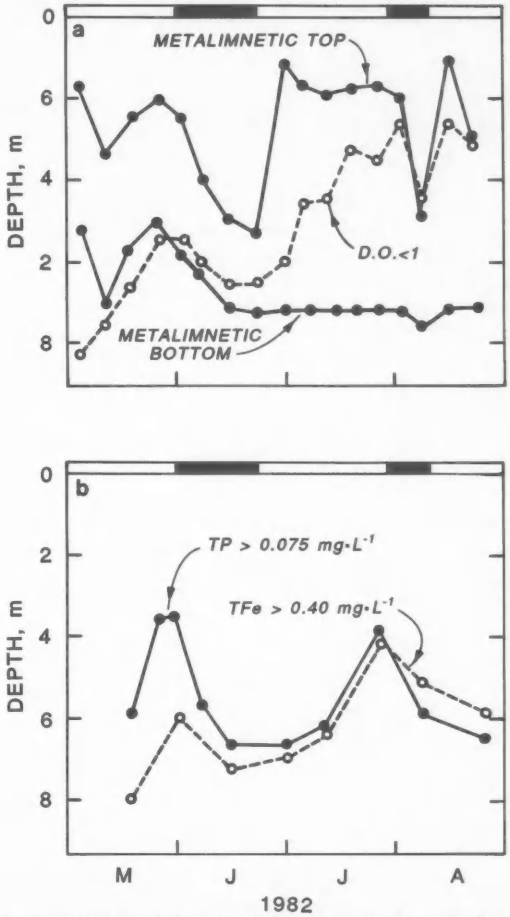

FIG. 8. Seasonal variations in (a) the upper and lower metalimnetic boundries and the isoline where dissolved oxygen (DO) was <1.0 mg·L^{-1} and (b) the isolines (within the metalimnion or hypolimnion) where TP was >0.075 mg·L^{-1} and TFe was >0.40 mg·L^{-1}.

and sedimentation of P. Nurnberg (1984) suggested that 30% of the hypolimnetic P in Lake Magog became adsorbed onto oxidized Fe complexes during autumnal overturn, while 60% was either incorporated into phytoplankton biomass or remained as SRP. Larson et al. (1981) reported that Shagawa Lake exhibited declines in TP mass, due to sedimentation, after partial overturns induced by high wind power that reoxygenated the hypolimnion.

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$^{210}Pb/^{226}Ra$ Determination of Longevity in Redfish

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Campana, S. E., K. C. T. Zwanenburg, and J. N. Smith. 1990. $^{210}Pb/^{226}Ra$ determination of longevity in redfish. Can. J. Fish. Aquat. Sci. 47: 163–165.

Examination of annular growth rings apparent in charred otolith cross sections is the basis for reports of extreme longevity in the rockfish genus *Sebastes*, but the interpretation of the annuli has long been disputed. We used a radiochemical assay of the otolith core to confirm our interpretation of annuli in Atlantic redfish, *Sebastes mentella*, to at least an age of 65 yr. Through measurement of the radioactive disequilibrium between ^{226}Ra and ^{210}Pb, it appears that redfish live to an age of at least 75 yr in the waters off of Nova Scotia.

Les données sur l'extrême longévité des sébastes du genre *Sebastes* proviennent de l'examen des anneaux de croissance annuelle visibles dans des coupes transversales d'otolithe brulées. Toutefois, l'interprétation des annuli a longtemps fait l'objet d'une controverse. Un examen radiochimique du noyau de l'otolithe a permis de confirmer notre interprétation des annuli chez le sébaste atlantique (*Sebastes mentella*) jusqu'à au moins 65 ans. D'après la quantification du déséquilibre radioactif entre Ra^{226} et Pb^{210}, il semble que le sébaste atteint au moins 75 an dans les eaux hauturières de la Nouvelle-Écosse.

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Several north temperate fish species are reputed to have lifespans over 60 yr (Power 1978; Beamish and Chilton 1982; Chilton and Beamish 1982; Beamish and McFarlane 1985), but the reported maximum ages have varied widely depending upon the choice of ageing methodologies and the interpretation of the investigator (Boehlert and Yoklavich 1984; Campana 1984). Recent findings indicate that annular growth rings apparent on scales and the surface of otoliths can underestimate the true age of old fishes by up to a factor of three (Beamish 1979; Casselman 1987). Such errors can confound any attempt at optimal management of a fish stock. Examination of charred otolith cross sections is now the preferred age determination technique for many species, but controversy concerning the interpretation of annuli remains (NAFO 1983; ICES 1984). Through recapture of tagged fish, annulus formation up to an age of 34 yr has been validated in the rockfish genus *Sebastes* (Leaman and Nagtegaal 1987). Unfortunately, the most controversial age determinations have usually been associated with fish that are much older. In a seminal study, Bennett et al. (1982) conducted a radiochemical assay of entire otoliths, concluding that *Sebastes diploproa* lived to considerably greater ages than was indicated by annuli visible on the otolith surface. In demonstrating the potential power of their age determination methodology, these authors highlighted the relative imprecision of ^{210}Pb:^{226}Ra ratios when applied to entire otoliths. We avoided a number of sources of potential error, and increased the precision of this geochronological technique by restricting the analysis to the extracted otolith core. Through use of a series of age-stratified samples, we used the ^{210}Pb:^{226}Ra ratio in the otolith core as a radiochemical clock to test our interpretation of annuli in Atlantic redfish, *Sebastes mentella*.

Materials and Methods

Redfish were collected from depths of 200–900 m along the edge of the Scotian Shelf in October, 1985 and 1986 (Zwanenburg and Hurley 1987). Sagittal otolith pairs ($n = 2775$) were extracted from fresh specimens and stored dry in paper envelopes. One otolith from each pair was cracked, charred, and coated with oil for the determination of fish age (Christensen 1964). Annuli were counted under 50× magnification at least twice by each of two independent readers, using criteria established by Beamish (1979). The remaining otolith from fish of age categories 6, 10–15, 20–25, 30–35, 40–45, 50–55, and 60+ yr were selected for core extraction and radiochemical analysis.

Otolith cores were extracted as rectangular blocks centred around the otolith nucleus. The location of the nucleus was assessed in relation to intact otolith morphology, and confirmed through sectioning of test samples. Block dimensions ($6.3 \times 3.2 \times 0.94$ mm) were derived from measurements of 5-yr old sagittae (length, width, and thickness, mean (SD) = 6.33 (0.12), 3.62 (0.51), and 0.95 (0.12) mm, respectively; $n = 18$). While a block is a crude approximation of otolith shape, the relatively large annuli in young otoliths imply that slight errors in measurement or extraction would have little effect on the mean age of the core. Cores were isolated with a low-speed, diamond-bladed saw, thinned with a metallurgical polishing machine, and cleansed of surface residue. Cores were subse-

TABLE 1. Radionuclide measurements on otolith cores. $^{210}P_o$ and $^{208}P_o$ tracer-plated silver discs were counted 3–4 wk in an alpha spectrometer to obtain the count statistics. The mean ^{226}Ra activity (five whole otolith samples, approximately 13 g each) was 0.033 ± 0.002 dpm/g. Data are given with 1 sigma counting uncertainties. Sample ages were derived from annulus counts of the otolith, and incorporated the time between sampling and radiochemical analysis.

Mean sample age (yr)	^{210}Pb (dpm/g)	^{210}Pb/^{226}Ra (dpm/g)
8.4	0.0077 ± 0.0012	0.233 ± 0.039
14.1	0.0103 ± 0.0015	0.312 ± 0.049
24.8	0.0197 ± 0.0036	0.597 ± 0.115
33.8	0.0182 ± 0.0023	0.552 ± 0.077
44.8	0.0260 ± 0.0031	0.788 ± 0.105
54.2	0.0242 ± 0.0030	0.733 ± 0.101
65.0	0.0268 ± 0.0036	0.812 ± 0.120

quently pooled within age categories to form samples weighing approximately 1.0 g (21–28 cores).

The ^{210}Pb activity was determined by alpha spectrometric measurements of ^{210}Po, while ^{226}Ra was measured with a radon gas emanation technique (Smith and Walton 1980) as modified by Bennett et al. (1982) for otolith analyses. The ^{210}Pb blank was 0.0005 dpm and background counts were less than $1.0 \cdot d^{-1}$. ^{226}Ra analyses of both the core samples and 13 g whole-otolith samples ($n = 5$), revealed no significant differences in ^{226}Ra concentration between the two types of sample; therefore, the more precise whole-otolith ^{226}Ra values were used in calculations of ^{210}Pb ingrowth rates (Table 1). The otoliths were sufficiently old that ^{210}Po (half-life, 138 d) and ^{210}Pb would be in secular equilibrium, and sufficiently young for there to have been negligible decay of ^{226}Ra (half-life, 1608 yr).

To corroborate our annulus interpretations, we sent subsamples of our aged otoliths, stratified by age category, to three different age determination laboratories. All were experienced in interpreting *Sebastes* otoliths, and were given complete latitude in the criteria they adopted for age determination. The laboratories had no prior knowledge of our age assignments or categorization.

Results and Discussion

Otolith growth occurs through concentric accretions of calcium carbonate which show no evidence of resorption after deposition (Campana and Neilson 1985). The basis for radiochemical age determination is the incorporation of the calcium analogue ^{226}Ra into the accreting crystalline structure. Since ^{226}Ra decays radioactively to ^{210}Pb (half-life, 22.3 yr), the ratio of the two isotopes is an index of elapsed time since ^{226}Ra incorporation. The ^{210}Pb isotope is particularly suited to the determination of fish age due to the similarity between its half-life and the longevity of a typical fish.

In the only other study of this kind, Bennett et al. (1982) analyzed entire otoliths, and thus were forced to model the continued accretion of ^{226}Ra with otolith growth, through models of otolith mass growth rate. Further, they assumed constancy in the ratio of incorporated ^{210}Pb:^{226}Ra with age. We largely avoided these potential sources of error by extracting the core of the otolith, as defined by the first five annuli. Assuming negligible migration of radionuclides across annulus boundaries, radium decay in the otolith core should reflect elapsed time since its formation, and thus be unaffected by subsequent otolith growth.

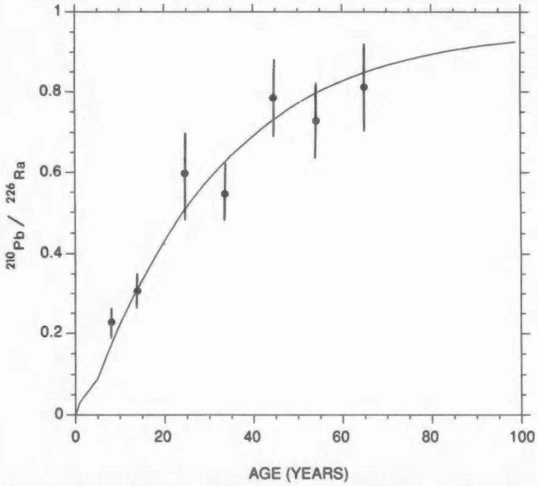

FIG. 1. Observed ^{210}Pb:^{226}Ra in otolith cores as a function of presumed otolith age. Error bars represent 1 SE. The decay curve expected of accurate age determinations represents simple first order ingrowth of ^{210}Pb with an initial ratio of zero. The first 5 yr of otolith growth were modelled assuming a linear increase in otolith mass with time and a constant radium incorporation rate.

Activity ratios of ^{210}Pb and ^{226}Ra, based upon simple ingrowth of ^{210}Pb in the fully-accreted otolith core, were used to estimate the age of the completed core. Assuming a linear increase in otolith mass through the period of core formation, the ratio, R_t, of the ^{210}Pb activity (A_{Pb}) to the ^{226}Ra activity (A_{Ra}) can be derived through integration of the standard rate equation for radioactive ingrowth and decay (Bennett et al. 1982), as in

$$(1) \quad R_{0 \leq t \leq 5} = \frac{A_{Pb}}{A_{Ra}}(t) = 1 - (1 - R^*)\,\frac{(1 - e^{-\lambda t})}{\lambda t},$$

where $0 \leq t(\text{years}) \leq 5$, λ is the radioactive decay constant ($0.031 \cdot yr^{-1}$) for ^{210}Pb, and R^* is the initial ^{210}Pb:^{226}Ra activity ratio in newly-formed otolith material. For $t > 5$ yr, R_t is given by

$$(2) \quad R_{5<t} = \frac{A_{Pb}}{A_{Ra}}(t) = (1 - e^{-\lambda(t-5)}) + R_{t=5},$$

where $R_{t=5}$ is given by equation (1). The relationship between R_t and otolith age for $R^* = 0$ is illustrated in Fig. 1. From their results with juvenile *Sebastes*, Bennett et al. (1982) concluded that $R^* < 0.2$, while the results of this study are consistent with $R^* < 0.1$. While we assumed here that there was negligible uptake of ^{210}Pb from seawater ($R^* = 0$), values of R^* as high as 0.2 would not alter the conclusions of this study.

The ^{210}Pb:^{226}Ra activity ratios in the otolith cores were consistent with the otolith ages determined by annular counts (Fig. 1). Hence, the analysis supports our criteria, as outlined by Beamish (1979), for the interpretation of otolith annuli. These criteria have been widely accepted by those ageing Pacific fishes (Chilton and Beamish 1982), but have been rejected by those ageing Atlantic species as inducing age overestimation (NAFO 1983; ICES 1984). Corroboration of our annulus interpretations was provided by the three independent age determination laboratories, all of whom confirmed our interpretations for otoliths

Table 2. Comparison of mean annulus counts in redfish otoliths made by three independent laboratories. All otoliths were initially examined for this study; age-stratified subsamples ($n = 15$) were subsequently sent to the other laboratories for corroboration. Laboratories A and B used criteria for annulus interpretation similar to ours; laboratory C did not.

Age category (yr)	This study	Laboratory A	Laboratory B	Laboratory C
10–15	11.7	13.7	8.5	12.3
30–35	31.4	27.3	28.5	25.7
40–45	42.4	41.7	44.7	26.7
50–55	52.0	48.7	50.0	27.5
60–65	63.1	64.3	54.0	27.0

less than 25 yr old (Table 2). However, only the laboratories using Beamish's (1979) criteria confirmed our ages for the older fish. The consistency between the ages based upon these criteria and the radiochemical assay indicates that previous suggestions of longevity in Atlantic redfish of 70 yr or more are well founded (Sandeman 1961). Our examinations identified individuals that are 75 yr old. Our results also indicate that current age determination practices for Atlantic redfish, both scale- and otolith-based, are appropriate only to an age of approximately 25 yr. Little credence has been given to the validity of the outer, narrow annuli under this regime (NAFO 1983; ICES 1984). Since the NAFO/ICES practices are based upon validated ages in young fish (<15 yr) (Kelly and Wolf 1959; Mayo et al. 1981), our results underline the importance of age validation across the entire age range of the species (Beamish and McFarlane 1983). Use of underestimated ages in ecological or fisheries management contexts artifactually increases apparent growth and mortality rates, and could result in suboptimal management of the resource.

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Effects of Fish Removal on the Limnetic Ecosystem of a Eutrophic Lake

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The effects of fish elimination in the eutrophic Lake Haugatjern, Sør-Trøndelag County, Norway, were studied during 1979–84. Total elimination of the fish populations by rotenone in late 1980 resulted in a fourfold decrease in the algal biomass. The species composition changed from a dominance by the large-sized *Anabaena flos-aquae* and *Staurastrum luetkemuelleri* to smaller, fast-growing species and gelatinous green algae. The total zooplankton biomass remained at the same level in all years, but while the rotifers almost disappeared after the rotenone treatment, the daphnids increased their share of the biomass from 49–63% during 1979–80 to 74–90% during 1982–84. The mean individual size of the adult daphnids increased in the same period from 1.3 to 1.8 mm. A 30% drop in the total phosphorus concentration in the lake after the biomanipulation was explained by increased sedimentation of zooplankton and reduced phosphorus release from the epilimnetic sediments because of the lowered pH. The fish elimination also resulted in a lower yield of biomass per unit of phosphorus in the lake.

De 1979 à 1984, nous avons étudié les effets de la destruction de la population de poissons du lac Haugatjern, un lac eutrophe du comté de Sør-Trøndelag en Norvège. La destruction totale des populations de poissons par la roténone vers la fin de l'année 1980 a fait chuter la biomasse d'algues par un facteur de 4. La composition des espèces d'algues a été modifiée : les espèces dominantes de grande taille *Anabaena flos-aquae* et *Staurastrum luetkemuelleri* ont été remplacées par des algues plus petites à croissance rapide et par des algues vertes gélatineuses. La biomasse zooplanctonique totale est restée la même durant toutes ces années, mais, tandis que les rotifères ont presque complètement disparus après le traitement à la roténone, la proportion de daphnées a augmenté, passant de 49–63 % en 1979–80 à 74–90 % en 1982–84. La taille moyenne des daphnées adultes a augmenté de 1,3 à 1,8 mm durant cette même période. Nous pensons que la chute de 30 % de la concentration en phosphore total suite au traitement a été causée par une augmentation de la sédimentation du zooplancton et une diminution de la libération de phosphore par les sédiments épilimnétiques due à l'abaissement du pH. La destruction des populations de poissons a aussi entraîné un abaissement de la production de biomasse par unité de phosphore dans le lac.

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Experiments in eutrophic lakes and ponds have revealed that a decrease in the stock of planktivorous fish may cause a reduction of the algal biomass (Hrbáček et al. 1961; Andersson et al. 1978; Stenson et al. 1978; Leah et al. 1980; Shapiro et al. 1982; Shapiro and Wright 1984; Reinertsen et al. 1986; Carpenter et al. 1987). Removal of planktivorous fish has therefore been proposed as a method to improve the water quality in eutrophicated lakes. The effects of this kind of biomanipulation need to be tested in long-term lake experiments, and the present study was carried out to investigate the effect of fish elimination in a eutrophicated lake over several years and to elucidate important mechanisms involved in the oligotrophication process.

Materials and Methods

The experiment was performed in Lake Haugatjern (area 0.091 km^2, mean depth 7.6 m), central Norway (63°29′N,

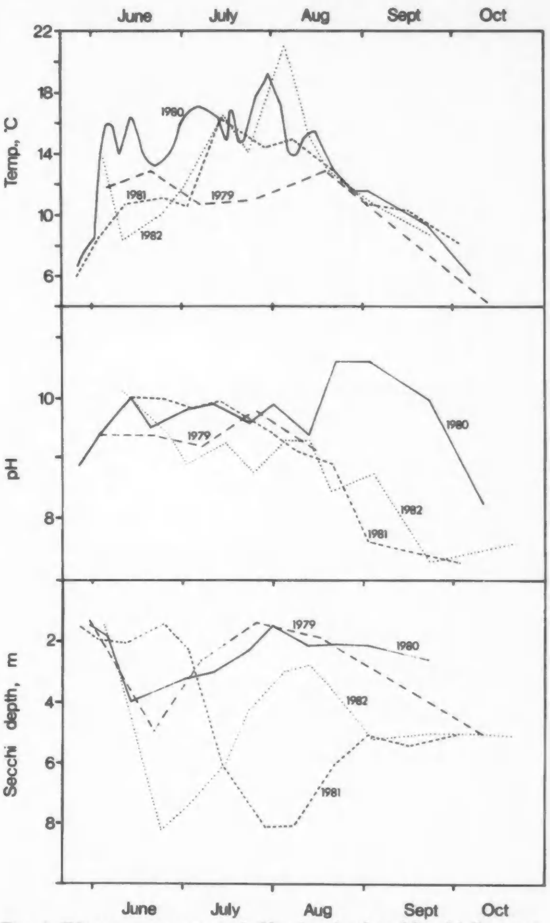

FIG. 1. Water temperatures and pH at 1 m depth and Secchi disc transparency during 1979–82.

11°52′E, 697 m above sea level) during 1979–84. The drainage area (1.5 km^2) is mostly covered with heather and birch, but about 0.23 km^2 of the area is cultivated.

The lake has no visible outlet and the estimated water retention time of 2.9 yr implies that 30% of the water supplied to the drainage area reached the lake (Langeland 1982a). Melting snow is the most important water source (Jacobsen 1974).

Lake Haugatjern is known for its extraordinary high yield of whitefish (*Coregonus lavaretus*). An average catch of more than 400 kg·ha^{-1}·yr^{-1} has been obtained at times (Huitfeldt-Kaas 1934). During the 1970s, catches seemed to have varied from approximately 50 to 100 kg·ha^{-1}·yr^{-1}.

The lake was treated with 350 L of rotenone solution (ProNoxfish), corresponding to nearly 0.5 mg·L lake water^{-1}, on 22 September 1980. All the fish were killed by the treatment, and the total catch in 1980, obtained by net fishing during summer and by collecting dead fish at the water surface and along the shores just after the rotenone treatment, amounted to 165 kg·ha^{-1}. The catch comprised mainly whitefish, with some perch (*Perca fluviatilis*) and brown trout (*Salmo trutta*), 12 and 4 kg·ha^{-1}, respectively. The lake was restocked in the spring of 1982 with 3500 Arctic char (*Salvelinus alpinus*) fry and with 5000 more in 1983 and 1984.

Water samples for chemical analyses and phytoplankton counting during 1979–82 were taken at depths of 0.2, 1, 3, 5, 7, 10, 12, and 14 m with a tube sampler (length 1 m, volume 1.3 L). In 1983 and 1984, the water samples for phytoplankton counting were taken at 1-m intervals and treated as mixed samples from 0–5 and 5–10 m. Zooplankton were sampled from 0–14 m depth at 1-m intervals with a 5-L cylindrical tube sampler (length 1 m). The samples were filtered through a plankton net (mesh size 45 μm).

Temperature and pH were measured in situ with a Montedoro–Whitney digital pH meter (model DPG-1B). Secchi disc transparency was determined with a 25-cm-diameter Secchi disc.

Samples for determination of total dissolved nitrogen (TSN), total dissolved phosphorus (TSP), soluble reactive phosphorus (SRP), and nitrate (NO_3-N) were filtered through preignited Whatman GF/C filters and preserved with two or three drops of chloroform (nitrogen samples) or 2.5 mL of 9 N H_2SO_4 (phosphorus samples) per 250-mL sample. The concentration of TSP was determined as SRP after digestion with acid persulfate for 30 min at 120°C (Koroleff 1976a). Analyses of TSN and NO_3-N were performed according to Koroleff (1976b) and Grasshoff (1976), respectively. Samples for determination of particulate carbon (PC) and phosphorus (PP) were prefiltered through a 140-μm screen to remove larger-sized zooplankton, after which the samples were collected on Whatman GF/C filters and stored at −18°C until analysis. PP was determined as TSP after grinding the glass-fiber samples in distilled water, digestion at 120°C, and filtering the digested mixture to remove the glass fibers. PC was determined in a Carlo Erba CHN-analyzer (model 1104) after treatment of the samples with acidic fumes to remove carbonate.

Nine intact sediment cores for exchange experiments were obtained from the epilimnion area by a gravity corer on 24 September 1985. The cores were placed in thermostated waterbaths (8°C, lake temperature) and incubated in the dark. The water above the sediment was stirred by a magnetic stirrer. NaOH (0.1–1 M) was added once a day to keep the pH at a stable level. The experiment lasted 5 d and 40 mL was removed daily and filtered (GF/C) before analysis of SRP.

Samples for phytoplankton counting were preserved with acid Lugol's solution and counted in an inverted microscope. Samples of *Anabaena flos-aquae* were sonicated to break up the colonies and counted separately. The fresh weight of the algal samples was estimated from geometric models assuming a specific gravity of 1.0 mg·mm^{-3}. Conversion to carbon from biovolume was made with a factor of 0.28 pg C·μm^{-3} for the cryptophytes (unpubl. results) and 0.14 pg C·μm^{-3} for the other algal groups (Olsen et al. 1983). Algal biomass was converted to chlorophyll *a* (Chl *a*) by assuming that 1 mg of C was equivalent to 11 μg of Chl *a* (unpubl. results).

The zooplankton samples were fixed with acid Lugol's solution. The biomass was calculated according to Bottrell et al. (1976) and Langeland (1982b) using length/weight regressions. The dry weight was assumed to be 10% of the wet weight and the carbon content 40% of dry weight (Langeland 1982b). The phosphorus content of the zooplankton was considered to be 3% by weight of the carbon content (Langeland et al. 1985).

Sedimented material was collected during the summer stagnation period in parallel traps (length 27 cm, volume 1.7 L) in the upper metalimnion (3–6 m depth). The traps contained 25

TABLE 1. Mean (±1 SE) concentrations ($\mu g \cdot L^{-1}$) of different fractions of phosphorus and nitrogen in the 0–10 m layer for the period early June – late September 1979–82.

Year	TSP	PP	NO_3–N	TSN	PN
1979	19.5±4.0 n = 24	17.8±1.4 n = 27	3.5±0.5 n = 24	207±10 n = 30	210±14 n = 30
1980	24.1±2.6 n = 64	18.0±1.1 n = 76	2.9±0.6 n = 60	666±79 n = 21	158±8 n = 65
1981	17.5±2.1 N = 40	—[a]	4.8±0.5 n = 39	583±130 n = 10	—[a]
1982	20.5±1.0 n = 35	9.4±1.2 n = 44	12.2±2.1 n = 24	236±61 n = 8	132±13 n = 40

[a] Not measured.

TABLE 2. Release of SRP from the 0–3 and 3–6 m layer of the epilimnic sediments (mg $P \cdot m^{-2} \cdot d^{-1}$) during June–September. The area as percentage of the total lake surface is given in brackets.

Depth	1979	1980	1981	1982
0–3 m (31%)	0.34	0.68	0.19	0.16
3–6 m (21%)	0.19	0.15	0.13	0.08
Total	0.53	0.83	0.32	0.24

mL of formaldehyde to preserve the collected material throughout the 7- to 10-d sampling periods.

Results

Lake Haugatjern is a dimictic lake. The circulation periods occurred in early June and in the first part of October, and the thermocline moved from 4 to 7 m depth during the summer period. The mean temperature at 1 m depth during the period June–September varied between 12.5 and 15.0°C during 1979–81, with the highest mean in 1980 (Fig. 1).

Prior to the rotenone treatment, pH in the epilimnion varied between 9.2 and 10.6 in the summer period, with the highest values in late August 1980 (Fig. 1). In the years after the rotenone treatment, pH was high (9.3–10.0) during the early summer period, decreased in August, and reached a value of 7.4 in late September. Secchi disc transparency never exceeded 5 m prior to the biomanipulation whereas the maximum transparency in the following years was 8.1 m (Fig. 1). The mean transparency during 1979–82 was 2.8 (n = 6), 2.4 (n = 11), 4.8 (n = 12), and 4.6 m (n = 13), respectively.

Anoxic conditions during 1979–82 were recorded below 3 and 10 m depth at the end of the winter and summer stagnation periods, respectively. Values of 1.0 mg $TSP \cdot L^{-1}$ and 3.8 mg $TSN \cdot L^{-1}$ were measured at 14 m depth before ice-break in late May 1979. In early September during 1980–82 the maximum concentrations of TSP and TSN in the hypolimnion were 0.4 and 2.0 $mg \cdot L^{-1}$, respectively.

A significant ($p < 0.05$) decrease in the concentration of PP in the 0–10 m layer was observed in 1982 compared with earlier years (Table 1). The concentration of TSP was at about the same level, 17–24 $\mu g \cdot L^{-1}$, in all years. The concentrations of PN and TSN were relatively high, throughout, and the nitrogen to phosphorus ratios of the soluble and particulate fractions were 10–35 and 9–21 (weight), respectively.

An expression of the release of phosphorus from the epilimnic sediments as a function of pH was obtained in laboratory experiments and can be expressed by the equation

$$(1)\quad F = (9.3 \times 10^{-4})\, e^{0.867\,(\mathrm{pH})} - 1$$

where F denotes the release rate (milligrams phosphorus per square metre per day). It predicts that a change in pH from 10.5 to 8.5, which took place in the late summer period in the years following the rotenone treatment (Fig. 1), will cause a decrease in the release rate from 3.2 to 0.6 mg $P \cdot m^{-2} \cdot d^{-1}$. The total pH-linked release of phosphorus from the epilimnic sediments in the summer periods during 1979–82 was reduced about 60% by the biomanipulation (Table 2). Changes in release rates below 6 m depth did not take place as the pH remained unaltered.

The sedimented material was fractionated from July 1981 because zooplankton became a large part of the sedimented material (Table 3). Throughout the prerotenone years, the fraction of zooplankton in the sediment was insignificant. The results revealed a significant ($p < 0.05$) decrease, 30%, in the phosphorus sedimentation rate from 1979–80 to 1982. Phos-

TABLE 3. Mean (±1 SE) sedimentation rate (total and fraction > 95 μm) of particulate phosphorus (mg $P \cdot m^{-2} \cdot d^{-1}$) and carbon (g $C \cdot m^{-2} \cdot d^{-1}$) for the epilimnion area calculated for the period July–September.

	1979	1980	1981	1982
Phosphorus				
Total	5.5±0.6	5.5±0.6	5.0±1.2	4.0±0.6
Fraction >95 μm	—[a]	—[a]	2.9±0.4	1.5±0.2
Carbon				
Total	0.72±0.06	0.70±0.15	0.41±0.07	0.47±0.06
Fraction >95 μm	—[a]	—[a]	0.18±0.05	0.17±0.01

[a] Not measured.

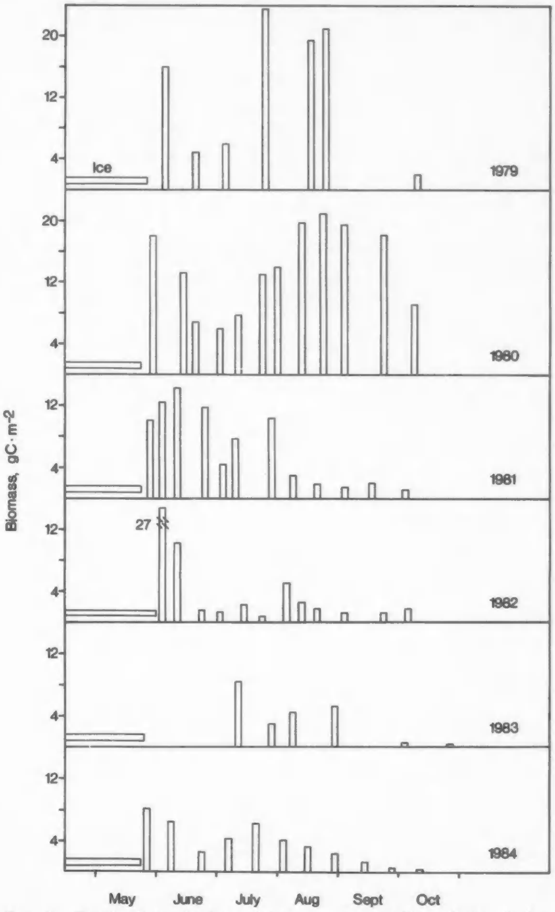

FIG. 2. Total phytoplankton biomass at sampling dates during 1979–84.

phorus bound in the larger-sized fraction (zooplankton) constituted approximately 60 and 40% of the total sedimented phosphorus in 1981 and 1982, respectively. The sedimentation rate of carbon decreased significantly ($p < 0.05$) after the rotenone treatment. About 40% of the sedimented carbon resided in the larger-sized fraction in 1981–82.

The external load of phosphorus (P-in) was calculated according to Berge (1987):

$$(2)\quad \text{P-in} = 2293 \times Q \times \text{P-tot} \times \text{Tw-0.16}$$

where Q is the yearly volume of water supplied to the lake, P-tot is the total concentration of phosphorus in the water, and Tw is the water retention time. Considering a total phosphorus concentration of 25 $\mu g \cdot L^{-1}$ (mean epilimnion concentration), the annual phosphorus load amounted to 0.17 mg $P \cdot m^{-2} \cdot d^{-1}$.

The estimated phosphorus load is assumed to be a maximum because the water is drained from the lake through the ground and not through a surface outlet. This will probably increase the retention time of phosphorus in the lake. On the assumption that the concentration of dissolved phosphorus is rather constant from one year to another (cf. Table 1), P-in can also be calculated as the amount of soluble phosphorus present in the water that leaves the lake throughout one year. This volume is equal to the volume supplied to the lake. If the concentration of dissolved phosphorus is 13 μg $P \cdot L^{-1}$ (cf. Table 1), P-in is 0.09 mg $P \cdot m^{-2} \cdot d^{-1}$.

The phytoplankton development during 1979–84 (Fig. 2; Table 4) revealed a pronounced decrease in the summer phytoplankton biomass after the rotenone treatment. In the years 1981–84 the mean total biomass decreased by a factor of 4 compared with the biomass in the prerotenone years.

The spring phytoplankton peak developed just after ice-break in late May each year (Fig. 2). The sampling frequency was insufficient to cover the maximum biomass which developed during this growth period. The results, however, show that the duration of the spring peak was about 2 wk longer in 1981, the year following the rotenone treatment. The diatom *Stephanodiscus rotula*, the green algae *Dictyosphaerium pulchellum* and *Chlamydomonas* sp., and the cryptophytes *Rhodomonas lacustris, Cryptomonas marssonii* and *C. ovata* were the dominating algal species during the spring peak (Reinertsen and Olsen 1984). The algal composition through the summer period was changed by the biomanipulation (Table 5). In 1979 and 1980 the blue-green algae *A. flos-aquae* and the green algae *Staurastrum luetkemuelleri* constituted more than 95% of the total summer biomass, respectively. *Anabaena flos-aquae* was also present in the postrotenone years, along with an increased dominance of small-sized species. Several species of cryptophytes were abundant, together with the green algal species *Ankyra judai* and *Oocystis lacustris*. Large-sized or colony-forming green algae such as *Sphaerocystis schroeteri, D. pulchellum*, and *S. luetkemuelleri* were also present after the biomanipulation, but in smaller amounts (Reinertsen and Olsen 1984). The latter species and *A. flos-aquae* are considered to be rather unavailable for the zooplankton (Reinertsen et al. 1986). However, the *Anabaena* colonies were much smaller in the postrotenone years than in 1979–80.

The mean total zooplankton biomass for the pre- and postrotenone years was 1.2 and 1.3 g $C \cdot m^{-2}$, respectively. The seasonal development was somewhat delayed in 1981 (Fig. 3), which can be an effect of the rotenone treatment in 1980. However, the cladoceran biomass was restored during the summer of 1981 (Fig. 3) and reached a level slightly above that of the prerotenone years. Cladocerans, mainly *Daphnia galeata*, constituted 49–63 and 74–90% of the zooplankton biomass before and after the fish elimination, respectively (Table 5). In 1979 and 1980, individuals of *D. galeata* larger than 1.4 mm were only recorded occasionally, while the fraction made up 40–50% of the population biomass in the subsequent years (Fig. 4). A smaller proportion of females reached a length of 2.5–2.8 mm. Individuals larger than 1.6 mm were never observed in the prerotenone years. The mean lengths of egg-carrying females during 1979–84 were 1.3, 1.3, 2.2, 1.8, 1.8, and 1.8 mm, respectively.

Bosmina longispina represented 3–7% of the total zooplankton biomass in the prerotenone years, but composed only 0.02–0.2% of total biomass during 1981–84. *Chydorus sphaericus*, which is mainly a littoral species, constituted 1–3% of the total biomass in 1979–80, despite its small individual size. The species was not found in the pelagic zone in the subsequent years.

The copepod biomass was reduced by approximately 40% during 1981–83 compared with the prerotenone years, but in 1984 it averaged 0.3 g $C \cdot m^{-2}$, which equalled the level of 1979–80 (Table 5). Of the two copepod species in the lake, *Diaptomus denticornis* and *Cyclops scutifer*, the former species

TABLE 4. Mean biomass of different algal groups (mg C·L^{-1}) and mean total biomass (0–10 m) in the summer stagnation period (early June–September).

	1979	1980	1981	1982	1983	1984
Blue-green algae	1.33	0.20	0.05	0.07	0.17	0.11
Green algae	0.15	1.14	0.05	0.04	0.22	0.14
Cryptophytes	0.03	0.05	0.23	0.06	0.03	0.06
Others	—	0.02	0.11	0.02	—	0.03
Total	1.51	1.41	0.44	0.19	0.42	0.34
±1 SE of total	0.37	0.20	0.18	0.04	0.03	0.08

TABLE 5. Species composition of zooplankton in Lake Haugatjern, 1979–84. Numbers indicate percentage of total biomass.

	1979	1980	1981	1982	1983	1984
Daphnia galeata	53	45	48	74	90	74
Daphnia pulex	—	—	0.07	—	—	—
Bosmina longispina	7	3	0.2	0.1	0.02	0.07
Chydorüs sphaericus	3	1.2	0.02	—	—	—
Bythotrephes longimanus	0.01	—	0.3	0.7	0.1	0.2
Diaptomus denticornis	9	6	14	12	3.3	2.6
Cyclops scutifer	14	23	0.4	4.1	5.9	22
Cyclops indet.	0.1	0.02	—	—	0.23	0.8
Keratella quadrata	1.1	—	0.2	0.3	<0.01	0.08
Keratella cochlearis	3.7	5.1	—	0.7	0.01	0.33
Keratella hiemalis	0.3	3.0	—	—	—	—
Polyarthra sp.	4.8	11.3	20.0	6.5	<0.01	0.16
Filinia longiseta	0.02	2.1	10.2	0.1	0.01	<0.01
Kellicottia longispina	0.01	0.01	—	0.02	—	<0.01
Conochilus sp.	—	—	4.6	1.0	0.23	—
Brachionus sp.	3.2	0.26	0.05	0.02	—	0.05
Lecane sp.	—	—	—	—	—	0.05
Asplanchna sp.	0.1	0.56	1.5	0.04		
Cladocera total	63	49	49	75	90	74
Copepoda total	23	29	14	16	9	25
Rotatoria total	13	22	37	9	<1	1

was the quickest to reestablish a new population after the treatment. Already in 1981 its share of the total biomass was higher than in the prerotenone years. During 1982–84 the total biomass share of the species declined to 2.6% compared with 6–9% in 1979–80. The biomass of *C. scutifer* remained low in 1981 and 1982 but reached the level of the prerotenone years in 1984.

The biomass of the different rotifer species decreased drastically from 1982 to 1984 (Table 5). *Polyarthra* sp. composed 20% of total biomass in 1981 but declined to a biomass share less than 0.02% in 1983 and 1984. Species such as *Filinia longiseta, Keratella hiemalis*, and *Brachionus* sp. were not recorded at all in the last year of the investigation whereas *Lecana* sp. and *Conochilus* sp. were only recorded after the treatment.

Discussion

According to earlier investigations (Grytbakk 1972), dense blooms of *Ceratium hirundinella, Staurastrum* sp., and particularly *A. flos-aquae* have occurred regularly during the summer period in Haugatjern for more than two decades. The episodes observed by us in the years prior to the rotenone treatment were therefore typical of this lake.

The treatment itself eliminated all fish, and controlled restocking gave the lake a new fish population, the size of which was estimated from regular catches and growth data (J. I. Koksvik, in prep.). These changes in the fish stock were clearly reflected in the average size of the daphnids (Fig. 5), in good agreement with the size efficiency hypothesis (Brooks and Dodson 1965; Hall et al. 1976) and with other field work in Lake Haugatjern (Koksvik and Langeland 1987).

The rotenone treatment had no significant effect ($p < 0.05$) on the total biomass of the zooplankton except for a reduction seen in the first year mainly caused by a delayed recovery of *D. galeata*. The species composition of the zooplankton was, however, clearly affected, rotifers first losing their stronghold (during 1982) and almost disappearing (in 1983 and 1984) while *D. galeata* took over. The disappearance of the rotifers is best explained as a result of competitive exclusion by the larger and more efficient *D. galeata* (cf. Langeland and Reinertsen 1982; Burgi et al. 1979) which experienced improved food conditions and reduced fish predation.

The elimination of the fish populations gave a nearly fourfold decrease in the phytoplankton biomass in the lake and induced a stable change in the equilibrium between the biomasses of phytoplankton (P) and zooplankton (Z). The P/Z biomass ratio went from 12–13 during 1979–80 to 2–3 in the postrotenone

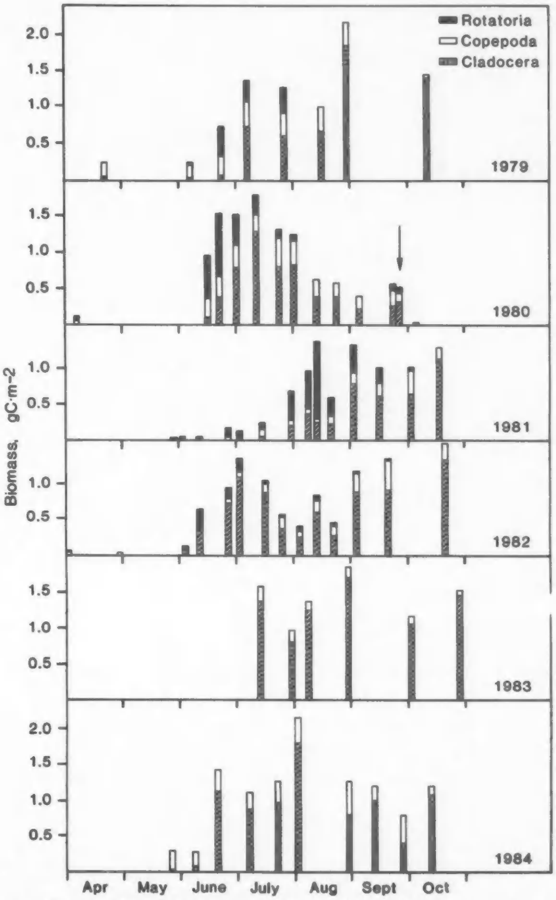

FIG. 3. Distribution of Rotatoria, Copepoda, and Cladocera at sampling dates during 1979–84. Rotenone treatment is indicated by the arrow.

years, and the new ratio was maintained after the moderate restocking of planktivorous fish in 1983 and 1984.

The increased dominance of large-sized zooplankton and the decreased P/Z biomass ratio indicate that the phytoplankton were exposed to a higher grazing pressure in the years following the biomanipulation and that a higher proportion of the primary production was transferred to the next trophic level. The higher grazing is indicated by an increased turnover rate of the phytoplankton (Reinertsen and Olsen 1984) as well as by the appearance of smaller, fast-growing cryptophyte species and *A. judai* and the increased dominance of gelatinous green algae such as *O. lacustris* and *S. schroeteri* (Fott 1975; Reinertsen and Langeland 1982; Porter 1977).

Nutrients are important for algal growth and phosphorus is the limiting element in Lake Haugatjern (Olsen et al. 1983). Turbulent diffusion and upwelling from the hypolimnion are expected to be the main nutrient sources in the lake because the external load (annual mean 0.17 mg P·m^{-2}·d^{-1}) and phosphorus release from the epilimnion sediments (0.24–0.83 mg·m^{-2}·d^{-1}, Table 2) together never exceeded 20% of the recorded sedimentation rates of phosphorus in the lake (5.5–4.0 mg·m^{-2}·d^{-1}, Table 3).

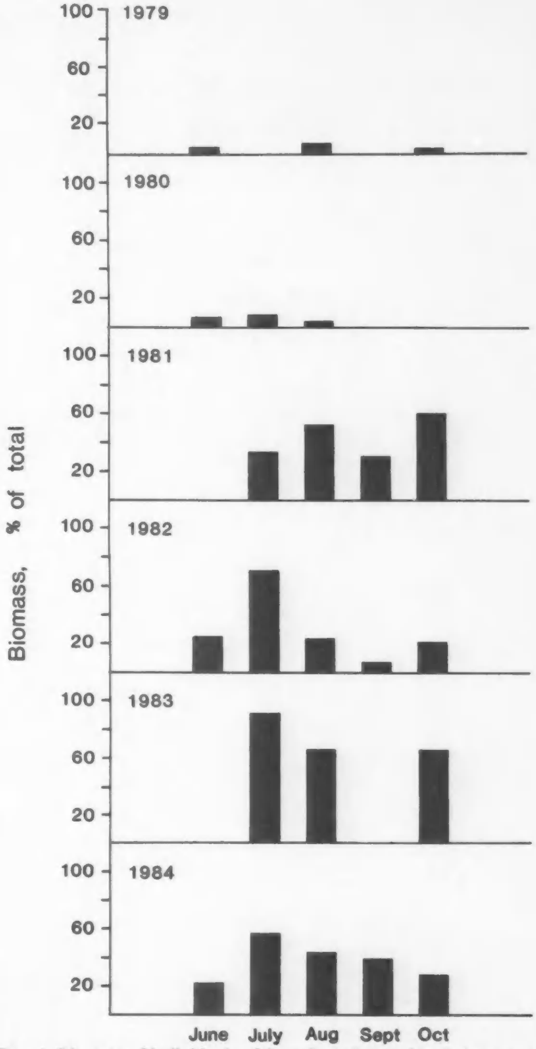

FIG. 4. Biomass of individuals of *D. galeata* larger than 1.4 mm as a percentage of the total Cladocera biomass.

The biomanipulation apparently led to a 30% reduction in the total phosphorus concentration in the lake (Table 6), and several factors may have been involved: (1) Reduced phosphorus release from the epilimnic sediments. (2) Increased zooplankton sedimentation rates (Table 3). The release of P from dead zooplankton is presumably delayed compared with that from algae. This would bring more phosphorus out of the cycling processes in the epilimnic zone as a result of the fish removal. (3) Reduced phosphorus excretion from the fish stock which amounted to about 2 mg·m^{-2}·d^{-1} (Olsen 1988).

The 30% reduction in total phosphorus in the lake water relates to a nearly 75% reduction in phytoplankton biomass and demonstrates that the yield of algal biomass per unit of phosphorus had changed. This is also illustrated in Fig. 6 which shows how the relationship between algal biomass and total phosphorus concentration changed because of fish removal. The

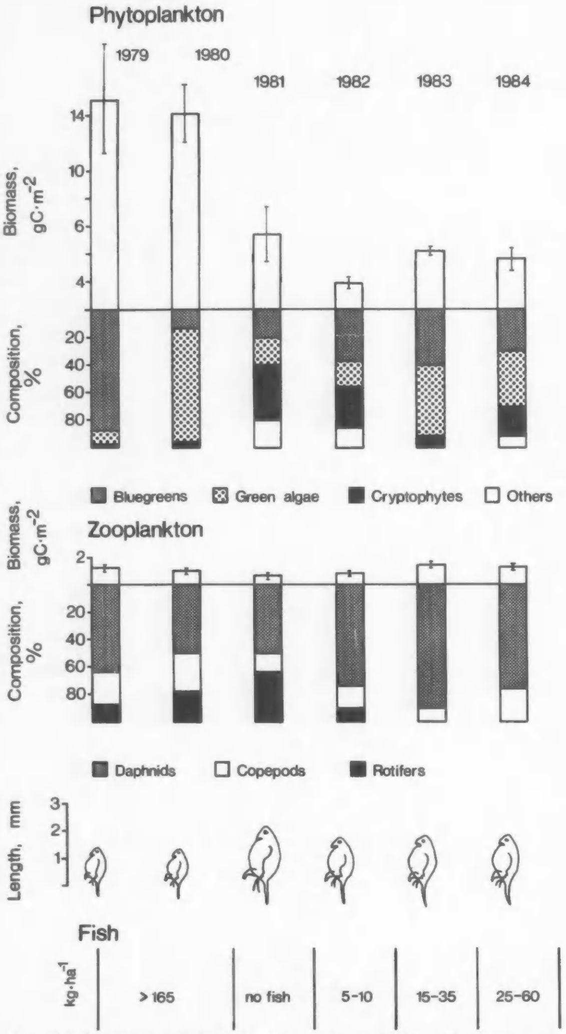

FIG. 5. Mean (± 1 SE) phytoplankton and zooplankton biomasses and composition (percentage of total biomass), mean individual size of daphnids, and estimated fish stock in Lake Haugatjern during 1979–84.

TABLE 6. Mean (± 1 SE) concentrations ($\mu g \cdot L^{-1}$) of different fractions of total phosphorus in the 0–10 m layer for the period early June – September 1979–82.

	1979	1980	1981	1982
Total soluble	19.5 ± 4.0 $n = 24$	24.1 ± 2.6 $n = 64$	17.5 ± 2.1 $n = 40$	20.3 ± 1.0 $n = 35$
Seston	17.8 ± 1.4 $n = 27$	18.0 ± 1.1 $n = 76$	12.0 ± 4.0[a]	9.4 ± 1.2 $n = 44$
Zooplankton	4.2 ± 0.8	3.3 ± 0.5	2.6 ± 0.5	2.9 ± 0.4
Total	41.5 ± 4.3	45.4 ± 2.9	32.1 ± 4.5	32.6 ± 1.6

[a] Estimated from phytoplankton biomass.

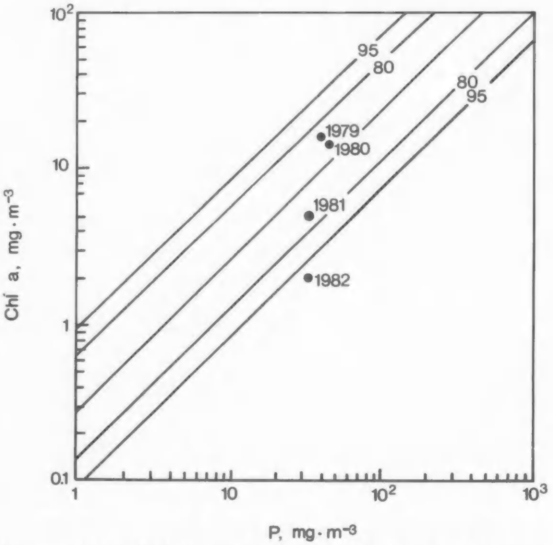

FIG. 6. Relationship between the mean annual Chl *a* concentrations and the mean annual total phosphorus concentrations in lakes worldwide (80 and 95% confidence limits, Janus and Vollenweider 1981) and in Lake Haugatjern during 1979–82.

values for the prerotenone years fit well with those expected for lakes of this trophic level. Upon biomanipulation the lake developed to a more oligotrophic state, i.e. less biomass was produced per unit of phosphorus in the years following the biomanipulation. This is an accordance with the increased phytoplankton turnover rate in the same years (Reinertsen and Olsen 1984), as the phosphorus to carbon ratio of algae increases with increasing growth rate (Olsen et al. 1983). In this particular case, the increased growth rate could be related to enhanced zooplankton grazing following the biomanipulation.

This study clearly demonstrates that a strong reduction of the planktivorous fish stock in a eutrophic lake gives a long-term reduction in algal biomass as long as the fish stock is kept under a critical level which allows the presence of large daphnids. A fish pertubation also affects the algal development through its alteration of the nutrient regime of the lake. Therefore, biotic structure in addition to nutrient loading must be taken into account in lake management.

Acknowledgments

This study forms part of the research program on eutrophication of inland waters financed by the Norwegian Council for Scientific and Industrial Research (NTNF). We thank Steinar Sanni for performing the studies of phosphorus release of sediment cores, Bente Rugstad, Marte Morkved, and Bjørn Ness for performing the chemical analyses, and Oddmund Brekke and Kjell Inge Reitan for counting phytoplankton.

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Intrapopulation Variation in the Breeding of Male Pink Salmon (*Oncorhynchus gorbuscha*) from a Lake Superior Tributary

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Noltie, D. B. 1990. Intrapopulation variation in the breeding of male pink salmon (*Oncorhynchus gorbuscha*) from a Lake Superior tributary. Can. J. Fish. Aquat. Sci. 47: 174–179.

Studies of breeding pink salmon (*Oncorhynchus gorbuscha*) from the Carp River, eastern Lake Superior, indicate that males seek fertilizations using two behavioural tactics. In 1985, a large run resulted in high breeding ground densities. During this run, males that resembled females were seen seeking fertilizations by sneaking rather than by competing for proximity to females. Morphological studies in 1985 confirmed the presence of males resembling females, their secondary sexual characters (hump height) being relatively less developed than in typical males. Although in poorer condition, such female-like males were reproductively mature, had returned to spawn at ages typical for this population, and had committed biomass to gonad no differently than had typical males. Furthermore, their spawning performance did not differ from typical males, as assessed both by the amount of gonad they retained unspawned at death and by their spawning ground life expectancies. In contrast, males attempting to sneak fertilizations were not observed during the small 1984 run when densities were low and males were generally in better condition than in 1985. Together, these results indicate that male pink salmon exhibit alternative breeding tactics. However, the demonstration of these tactics appears linked more to proximate factors (density and condition) than to divergent life history strategies as in other salmonid species.

Les résultats d'études sur la reproduction du saumon rose (*Oncorhynchus gorbuscha*) dans la rivière Carp (secteur est du lac Supérieur) révèlent que les mâles adoptent deux différents comportements au moment de l'accouplement. En 1985, une importante remontée a donné des densités élevées de reproducteurs dans les frayères. On a observé à ce moment des mâles ressemblant à des femelles qui cherchaient à s'accoupler en se glissant près des femelles au lieu de se les disputer. Les résultats d'études morphologiques menées en 1985 ont confirmé la présence de mâles ressemblant à des femelles : la hauteur de la bosse, caractère sexuel secondaire, était relativement moins élevée que chez les mâles typiques. Quoiqu'en plus mauvais état physique, ces mâles étaient prêts à la reproduction, étaient revenus frayer à un âge typique de cette population et montraient un rapport biomasse : poids des gonades semblable aux mâles typiques. De plus, leur performance à la fraie n'était pas différente de mâles typiques comme le révèle la quantité de gonades retenues à la mort et leur durée de vie dans les frayères. Par contre, aucun mâle cherchant à s'accoupler en se glissant près d'une femelle n'a été observé au cours de la faible remontée de 1984 quand les densités étaient faibles et que les mâles étaient généralement en meilleur état qu'en 1985. Globalement, ces résultats révèlent que le saumon rose mâle utilise deux différentes tactiques d'accouplement. Toutefois, la manifestation de ces tactiques semble liée plus étroitement à des facteurs immédiats (densité et état) qu'à différents cycles vitaux comme chez d'autres espèces de salmonidés.

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Alternative breeding patterns have been defined as "any discontinuous variation in an aspect of reproductive behavior among one sex in a single population with associated differences in the behaviors' costs and/or benefits" (Austad 1984). The Pacific salmon (genus *Oncorhynchus*) are one group where such dualities in male breeding tactics are known for populations of virtually all the congeners (e.g. Robertson 1957; Smirnov 1962; Hanson and Smith 1967; Schroder 1981; Leider et al. 1984; Gross 1985).

Pink salmon (*O. gorbuscha*) have thus far been the exceptions to this generalization, however: strong evidence for the occurrence of alternative male breeding patterns in this species has been lacking, and the suggestion that they may occur in some populations has only been recently put forth (Chebanov 1982; Keenleyside and Dupuis 1988a). Males which are "female-like" in their morphology have also been described in pink salmon, the suggestion being that "mimicking" females assists them in sneaking fertilizations and in avoiding competition (Kirkwood 1962; Beacham and Murray 1985). In addition, Davidson (1935) and Davidson and Shostrom (1936) reported finding male pink salmon whose humps were noticeably small for their lengths but whose snout development was typical for males their size.

Despite these indications, however, alternative male breeding patterns have not been the subject of specific investigation in pink salmon. This study (1) seeks behavioural and morphological evidence of the occurrence of alternative male breeding patterns in this species within a single stream over successive years, and (2) examines if and how aspects of the fish's ecology vary in accordance.

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Materials and Methods

Fish Capture and Measurement

The pink salmon studied were 1984 and 1985 spawners from the Carp River (46°57′N; 84°35′W), an eastern Lake Superior tributary 70 km north of Sault Ste. Marie, Ontario, and were descended from an inadvertent 1956 release at Thunder Bay (Kwain 1987a). Upstream migrants were captured daily below the spawning grounds by trap or gill net each year (see Noltie 1987 for details), the Julian catch date for each being noted. The 117 fish caught in 1984 (76 males, 41 females) constituted a substantially greater proportion of the run than did the 2115 caught in 1985 (1087 males, 1028 females; see Noltie 1987a).

Three morphological characters (body length, hump height, and total body weight) were measured for both males and females as outlined in Noltie (1987). Abdominal palpation and/or gamete extrusion was used to determine gender and evaluate male reproductive maturity (spermiating or nonspermiating). Noted also were marks inflicted by sea lamprey (*Petromyzon marinus*; see Noltie 1987) and the occurrence of overt thyroid hyperplasia (see Noltie 1988b; Noltie et al. 1988), each being associated with reduced condition. Once measured, each fish was tagged and released above the collection site. Some unspawned males in 1985 were retained for testis wet and dry weight determinations (see Noltie 1988b for methods). None bearing marks indicative of possible spawning involvement were included in analyses where body or gonad weights were concerned.

Daily spawning ground surveys were performed in 1985 to obtain the carcasses of tagged, spawned-out individuals and to determine their death dates and breeding lifespans. The testes of the males recovered were removed for assessment of testis depletion (see Noltie 1988b). The vertebral centra of particular individuals were also removed for aging (scales proved unreliable; see Noltie 1988a), some Lake Superior pink salmon maturing as non-2 yr olds (Wagner 1978; Wagner and Stauffer 1980; Nicolette 1984; Kwain and Kerr 1984; Kwain 1987b).

Behavioural Observations

Spawning groups in which egg deposition appeared imminent were observed on 22 different dates over both years, typically in the late afternoon and early evening when spawning activity peaked. Behaviours were recorded from a stream bank 3 to 5 m away (sometimes with aid of binoculars) by direct transcription and/or on video tape. Behavioural data were also collected during the daily spawning ground surveys and included (1) brief additional observations, (2) counts of group sizes and the sightings of lone males (those not associated with females), (3) records of the activities of males whose tag numbers were visible, and (4) rankings of the relative sizes and degree of hump development of males grouped around females.

Morphological Analyses

To determine how morphologically distinguishable the sexes were, discriminant analysis was applied to the ln-transformed body lengths and hump heights of males and females each year, these features being the species' most obviously differing external sexual characters. A priori group membership (true males and females) was assigned based on gonad characteristics. Males having a greater than 50% probability of being classified as females on the resulting discriminant axes were designated as "female-like," the remainder as "typical". Males of both designations were then examined for differences in characteristics other than those upon which the discriminant analyses were based.

Results

Spawning Milieu

1984

Spawners were few, and nesting females were scarce and isolated: of the 28 females about to spawn which were located on 22 day's spawning ground surveys in 1984, 78.6% were not within sight of another. Single, large, well-humped males actively monopolized these females and dispersed others seeking to associate with them: single males accompanied 17 (60.7%) of the 28 females, while groups of two, three, or four or more males accompanied the remaining five (17.9%), four (14.3%), and two (7.1%) females, respectively. Clusters were more prevalent where two or more nesting females were in close proximity, forming around 50% of the six females which nested near others (<5 m apart) but only around 36.5% of the 22 which nested in isolation (>15 m apart). Lone males were common on the spawning grounds in 1984: of 85 male sightings, 50% were individuals not actively associated with a nesting female. For tagged males individually identified on the spawning grounds, those seen at least once accompanying a nesting female were of significantly greater body length than were those only ever observed as lone individuals (males with females: 47.41 ± 0.86 cm, $n = 21$; lone males: 43.05 ± 1.77 cm, $n = 10$; $\bar{X} \pm$ SE; ANOVA $F = 6.30$, $p < 0.025$).

1985

Spawners were numerous and single males appeared unable to monopolize nesting females, the number grouped around females averaging 3.43 ($n = 134$ groups; SE = 0.13). Of 443 sightings of males on the spawning grounds, only 20% were of lone individuals, a rate significantly lower than recorded in 1984 (2×2 continuity-corrected $\chi^2 = 32.83$, 1 df, $p < 0.001$). Among tagged males which could be individually identified, the body lengths of those seen at least once accompanying nesting females did not differ from those observed only as lone individuals (males with females: 41.52 ± 0.40 cm, $n = 71$; lone males: 41.22 ± 0.74 cm, $n = 20$; $\bar{X} \pm 1$ SE; ANOVA $F = 0.12$, $p > 0.25$).

Behaviour

Cluster males

Males displayed two breeding tactics, the "cluster" tactic being the typical one. Cluster males were those which congregated in a staggered arrangement behind a nesting female. Competition among cluster males was intense, individuals jockeying to usurp positions closer to the female. Occupation of the lead (most forward) position within clusters reflected the outcome of such contests: in 96.4% of a sampling of 56 clusters, the lead male was as large or larger than any other cluster member. Lead males were also more frequent performers of the body quiver display (a spasmodic trembling of the entire body directed towards the prespawning female): in 102 occurrences from 14 clusters, less than 2% of those recorded were performed by other than the lead male. Extended parallel swim displays accompanied contests between cluster males of similar size, both individuals swimming rapidly upstream beside one another, matching each other's speed and direction.

Spawning by cluster males was preceded by repeated upstream swims by the female through her nest, accompanied by probes of the substrate with her anal fin and hesitation over the nest's deepest part. Cluster males responded to this by rushing upstream and closing ranks around the female, the lead male typically on one side, the foremost subsidiary male on the other, and the remaining cluster members flanking this trio. When actual egg deposition accompanied this, the female hesitated longer, gaped, and shed eggs, whereupon some or all the cluster males gaped and released sperm. Nest covering by the female immediately followed. Although most cluster males remained with the female once spawning was complete, large ones were apt to desert. The parallel swim and spawning observations derive from 43 h viewing of 33 groups of cluster males between 1984 and 1985. Additional details are presented in Noltie (1988a).

Outlier males

The second, less common breeding tactic observed was the "outlier" tactic. Outlier males held positions lateral to female-cluster male groupings, 1 to 1.5 m away, and just above the substrate (Fig. 1). This placed them nearer the female than some subsidiary cluster males. Outlier males were smaller than the cluster males attending a given female. They also exhibited minimal hump development, and thus resembled females in shape. Outlier males were seen only during 1985 where spawner densities were high. None were observed during the small 1984 run (although small males occasionally accompanied females for brief periods), nor did outlier males or large clusters of males accompany the few females which nested in isolation in 1985. Large, well-humped males were never seen as outliers.

Thirty-two hours were spent in 1985 intensely observing 23 clusters with which outlier males were associated. The number of cluster males comprising these groups averaged 3.41 (SE = 0.33). All but one of these were accompanied by a single outlier male, the remaining group with seven cluster males having two outliers. Outlier males were noncombative, retreating from approaches by cluster males and not performing parallel swims with or directing bites towards them. Despite this, outlier males were persistent in their association with particular clusters, returning quickly to the positions they retreated from. Although nested females usually acted territorially only towards other females, outlier males elicited similar responses, indicating possible gender misidentification. Body quivers by outlier males towards females were not seen.

During preliminary spawning activities, an outlier male's response to a female settling down into her nest was to dart laterally towards her. This allowed him to obtain a position more closely flanking the female than subsidiary cluster males approaching from downstream. Among the 14 actual egg depositions observed, outlier males obtained positions near females as successfully as they did during preliminary sequences. Because spawnings occurred near dusk, however, video recording could not be used to measure actual proximity. Noltie (1988a) presents additional details.

Morphology and Characteristics

Because tagging in 1985 was not universal, the morphology of most of the observed outlier males remained unknown. This

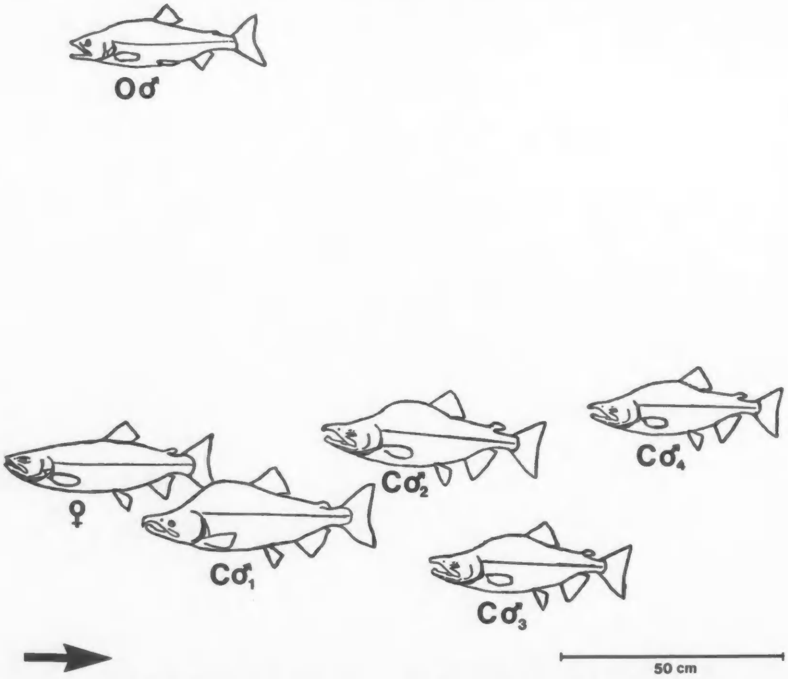

FIG. 1. Outline drawing of the relative positions of cluster (C) and outlier (O) males in a Carp River pink salmon spawning group. Arrow denotes direction of current flow. See text for further description.

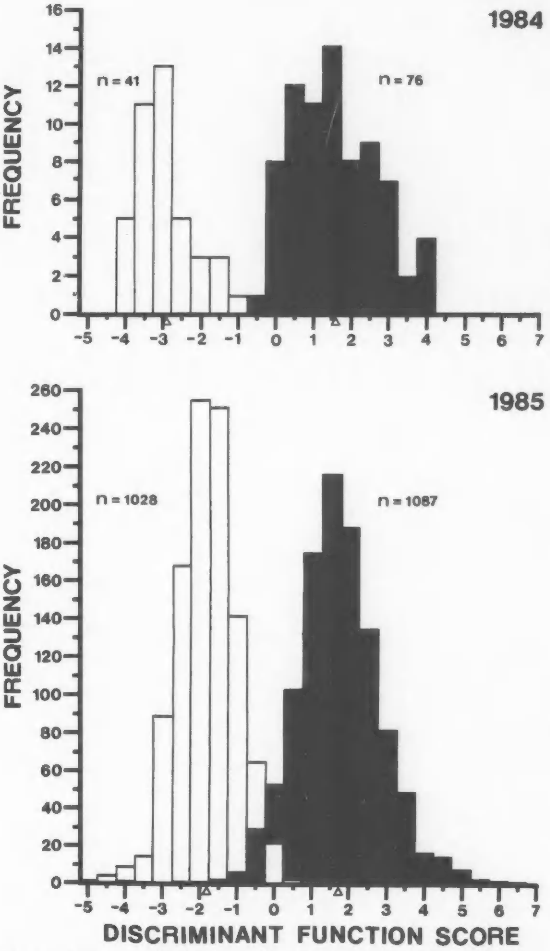

FIG. 2. Frequency distributions of male (black bars) and female (open bars) discriminant function scores from the 1984 (top) and 1985 (bottom) Carp River pink salmon morphological analyses. Smaller bars superimposed where distributions overlap. Group centroids shown on the abscissa. Standardized canonical discriminant function coefficients: 1984, ln(hump height) = 2.46095, ln(body length) = −2.19338; 1985, ln(hump height) = 1.69763, ln(body length) = −1.18626.

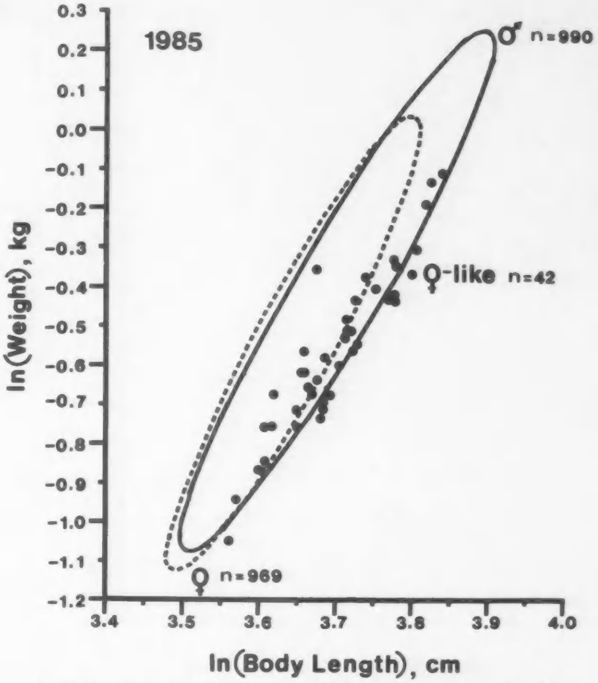

FIG. 3. Bivariate plot of the relationships between length and weight for all male (solid ellipse), female-like male (points), and female (dashed ellipse) 1985 Carp River pink salmon. Data summarized as 95% confidence ellipses for ease of display.

made impossible a direct comparison of their characteristics with those of cluster males. The observation that outlier males resembled females in appearance could be corroborated, however, by examining whether males resembling females in their morphology occurred among the catch obtained. For 1985, the discriminant analysis testing this indicated that differentiation of the sexes was significant ($\chi^2 = 2973.2$, df = 2, $p < 0.0001$) but incomplete: overlap between the male and female scorings (Fig. 2, bottom) revealed the presence of 59 "female-like" males (5.4%) whose morphology resembled that of females moreso than that of the remaining "typical" males. The unimodality in the male discriminant function scores (Fig. 2, bottom) indicated that this morphological variation was continuous, however. In contrast, for 1984 the differentiation of the sexes was both significant ($\chi^2 = 199.36$, df = 2, $p < 0.0001$) and complete, the male and female discriminant function scores not overlapping (Fig. 2, top).

Comparing their characteristics, the 1985 female-like males proved to be both significantly lighter than typical males (female-like males: 582 ± 20 g; typical males: 696 ± 7 g; $X \pm 1$ SE; ANOVA $F = 11.20$, $p < 0.001$) and in poorer condition (i.e. were light for their lengths; Fig. 3). Together these results imply that the males which resembled females in 1985 did so because of their lesser relative weights, this having prevented them from developing humps of sizes typical for their body lengths. Mean Julian catch date also differed significantly among the female-like males (259.23 ± 1.07, $n = 40$), typical males (256.50 ± 0.20, $n = 938$), and females (260.95 ± 0.22, $n = 952$) (ANOVA $F = 110.73$, $p < 0.0005$). A Student-Newman-Keuls test (Zar 1974) revealed that female-like males and females both approached the spawning grounds at similar times, their mean catch dates not differing ($p > 0.05$). In contrast, the catch dates of typical males differed significantly from both those of female-like males and females (both $p < 0.01$).

Tests of the following revealed no differences between female-like and typical males: (1) prespawning testis investment (relative gonad weight and composition); (2) proportion bearing immature gonads on capture; (3) length of breeding life; and (4) degree of postspawning testis depletion (relative gonad weight and composition) (see Noltie 1988a for details). Female-like morphology in 1985 could not be attributed to having sustained lamprey parasitism or to thyroid dysfunction: only 8.5% of the female-like males in 1985 bore lamprey marks (five of 59), while overt thyroid hyperplasia occurred in female-like and typical males with similar frequency (19 of 59 versus 371 of

1028; 2×2 continuity-corrected $\chi^2=0.22$, $p>0.50$). All female-like males in 1985 were typical 2-yr olds.

Discussion

The occurrence of alternative male breeding patterns may be understood from a game theory perspective (Maynard Smith 1982). Where individuals exhibit different pure strategies yielding equal fitness, the relative mix in the population may be an evolutionarily stable one (a mixed ESS) (Gross 1984, 1985; Maekawa and Hino 1986), disruptive selection acting to reinforce the contrasting fertilization tactics with differences in life history, morphology, and relative gonad investment. Alternatively, males may exhibit different breeding tactics conditional upon their status relative to other males: when at a competitive disadvantage, males may adopt an alternative tactic to make the best of a bad situation (Dawkins 1980; Gross 1984).

For pink salmon, considering the occurrence of the cluster and outlier tactics to be a mixed ESS appears inappropriate: although males which behaved as outliers did resemble females, those which were female-like in shape were neither morphologically distinct nor substantially different in their reproductive characteristics. Instead, the outlier fertilization tactic is likely employed facultatively by males to overcome the competitive disadvantages imposed by maturing at relatively low body weights for their lengths (low condition) and by having less somatic tissue to allocate to hump development (yielding a female-like appearance). This interpretation implies the synonymy of outlier and female-like males, a likely situation but one which would benefit from additional verification. Further testing would also resolve whether males can switch between tactics, and whether female-like characteristics are heritable.

Differences in spawner densities and male condition between years may account for the varying occurrence of outlier males. In 1984, the relative isolation of nesting females and their monopolization by single large males likely minimized the effectiveness of the outlier tactic. Males were also in generally good condition (Noltie 1990a), none exhibiting female-like morphology. In contrast, the high spawner densities of 1985, increased operational sex ratios, large clusters, and heightened male–male interaction apparently facilitated the outlier tactic. Males in 1985 were also in significantly poorer condition than in former years (Noltie 1990a), and some exhibited minimal secondary sexual character development, thereby appearing female-like. That high densities are needed for alternative male breeding tactics to be demonstrated and effective has been alluded to for many fishes (Warner and Robertson 1978; Warner and Hoffman 1980; Kodric-Brown 1981, 1988; Schroder 1981; Chebanov 1982; Dominey 1984). Density differences may also account for the varying occurrence and characteristics of lone males. At low densities, large inter-female distances and the monopolization of females by single large males together result in lone males being common and of small size, as was observed in 1984. At high densities, cluster formation resulting from the inability of males to monopolize females would diminish lone male numbers, as was observed in 1985. Similarity in the sizes of lone and cluster males would also be expected at high densities, the lone males that are observed likely being individuals in transition from one cluster to another instead of being smaller individuals excluded from clusters by competition.

The behaviour of the outlier male pink salmon was similar to the alternative male breeding behaviours exhibited by other salmonids. For example, the frequent attack of alternate males has been recorded many times, as has their avoidance of attacking typical males by executing quick retreats (Jones and King 1952; Hanson and Smith 1967; McCart 1970; Maekawa 1983) and the persistence of their association with female-typical male groupings (Jones and King 1952; Jones 1959, McCart 1970). As in pink salmon, the female-like appearance of alternate males in other species may explain why nesting females attack them (Hanson and Smith 1967; McCart 1970; Schroder 1981; Maekawa 1983).

Finally, the present work indicates that the general breeding behaviour of the introduced pink salmon of the Great Lakes differs little from that of anadromous individuals (Kuznetsov 1928; Semko 1939; Wickett 1959; Sheridan 1960; Kirkwood 1962; Strekalova 1963; Cameron 1968; Kamyshnaya and Smirnov 1968; Heard 1972; Smirnov 1975; Chebanov 1980, 1982; Keenleyside and Dupuis 1988a,b).

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Nighttime Pond Respiration Rate: Oxygen or Temperature Dependent?

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Madenjian, C. P. 1990. Nighttime pond respiration rate: oxygen or temperature dependent? Can. J. Fish. Aquat. Sci. 47: 180–183.

Two different models for the nighttime dissolved oxygen concentration (DO) dynamics in ponds were compared to determine which was more accurate. DO and water temperature were monitored overnight in marine shrimp (*Penaeus vannamei* and *P. monodon*) ponds; wind speed was also measured. The Whole Pond Respiration–Diffusion (WPRD) model, in which night respiration rate of the pond system is a function of water temperature, was fitted to observations of DO at dusk and approximately 3 h after dusk to generate predictions of pond DO at dawn. The Oláh model, which is based on respiration rate varying in direct proportion to DO, was also applied to the same set of DO observations to generate predictions of dawn DO. The mean absolute values of the residuals (the residual is equal to observed dawn DO minus predicted dawn DO) from applications of the WPRD and Oláh models were 0.39 and 0.77 mg $O_2 \cdot L^{-1}$, respectively, and the Oláh model showed consistent bias. The respiration rate of the pond system at night was therefore better described as a function of water temperature than as dependent on pond DO.

On compare deux modèles de la dynamique de la concentration nocturne d'oxygène dissous (DO) dans les eaux d'étang afin de déterminer laquelle est plus précise. On a déterminé la concentration de DO et la température de l'eau d'étangs peuplés de crevettes marines (*Penaeus vannamei* et *P. monodon*) au cours de la nuit, ainsi que la vitesse du vent. Le modèle respiration-diffusion pour l'étang entier (WPRD), où le taux de respiration nocturne du système aquatique est fonction de la température de l'eau, a été ajusté en fonction des données sur la concentration de DO relevées au crépuscule et environ trois heures après la tombée de la nuit afin d'obtenir des prédictions de la concentration de DO dans les eaux d'étang à l'aurore. On a aussi appliqué le modèle Olah, basé sur un taux de respiration qui varie en proportion directe à la concentration de DO, au même ensemble de données sur la concentration de DO afin d'obtenir des prédictions de la concentration de DO à l'aurore. Les valeurs absolues moyennes de la variance résiduelle (la variance résiduelle est égale à la concentration de DO observée à l'aurore moins la concentration de DO extrapolée à l'aurore) tirées des modèles WPRD et Olah s'élevaient respectivement à 0,39 et 0,77 mg O_2L^{-1} tandis que le modèle Olah montrait un biais uniforme. Le taux de respiration nocturne des eaux d'étang était donc mieux décrit conne ume fonction de la température de l'eau que dépendant de la concentration de DO dans l'eau d'étang.

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The study of the dynamics of dissolved oxygen concentration (DO) in aquaculture ponds is important in both basic and applied science contexts. Aquaculture ponds have served as model ecosystems for studying basic ecological processes, such as the succession of ecosystem net production (Madenjian 1988). In such studies, proper assessment of DO dynamics can be used to estimate the metabolic parameters of the pond system. From a practical standpoint, some understanding of the nighttime dynamics of pond DO is required to predict DO at dawn (Boyd et al. 1978; Romaire 1979; Madenjian et al. 1987a, 1987b, 1988). Such predictions may be used to better manage emergency aeration.

The nighttime respiration rate (respiration rate and oxygen consumption rate are used interchangeably in this paper) of ponds has usually been assumed to be independent of pond DO (Boyd et al. 1978; Romaire et al. 1978; Madenjian et al. 1987b, 1988). The Whole Pond Respiration–Diffusion (WPRD) model, in which pond respiration rate is solely dependent on water temperature, has yielded accurate predictions of dawn DO in freshwater and brackish water ponds under a wide range of wind conditions (Madenjian et al. 1987b, 1988). Meyer and Brune (1982) assumed the respiration rates of the water column and the pond sediments (the two major components of respiration in the pond) as independent of DO in their general model for a stillwater aquaculture pond.

In contrast, Oláh et al. (1978) modeled the daily cycle in fish pond DO by describing the pond respiration rate during the 24-h period as directly proportional to pond DO and as independent of water temperature. The respiration coefficient was estimated by fitting their model to nighttime observations of pond DO. Then, by accounting for primary production during the daytime, these researchers obtained accurate predictions of pond DO at the time of sunset the following day. All applications of the Oláh model have involved fitting the model to DO observations spanning a 24-h period; the Oláh model has not been applied to only nighttime data. Based on a DO-dependent respiration rate, Oláh et al. (1986) estimated primary production in fish ponds to elucidate patterns between primary production and fish production in the ponds.

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The purpose of this paper is to determine whether the nighttime pond respiration rate is more accurately depicted as DO dependent or as water temperature dependent. The performances of both models are evaluated and compared.

Models

The WPRD model consists of whole pond respiration and diffusion components (Madenjian et al. 1988):

$$(1)\quad \frac{d(\mathrm{DO})}{dt} = -ce^{kT} + \frac{\mathrm{KL}}{\mathrm{PD}}(\mathrm{SAT}(T,S) - \mathrm{DO})$$

where DO = pond DO (milligrams O_2 per litre), $d(\mathrm{DO})/dt$ = rate of change in pond DO with time (milligrams O_2 per litre per hour), c = respiration coefficient (milligrams O_2 per litre per hour), k = instantaneous rate of increases of respiration with water temperature (per degree Celsius), T = water temperature (degrees Celsius), KL = oxygen transfer coefficient (metres per hour), PD = average pond depth (metres), S = salinity (grams per kilogram), and $\mathrm{SAT}(T,S)$ = oxygen saturation level (milligrams O_2 per litre) at temperature T and salinity S. The constant k was set equal to $0.542 \cdot {}^{\circ}\mathrm{C}^{-1}$ (Madenjian et al. 1987b).

The Oláh model is represented as

$$(2)\quad \frac{d(\mathrm{DO})}{dt} = -R(\mathrm{DO}) + \frac{\mathrm{KL}}{\mathrm{PD}}(\mathrm{SAT}(T,S) - \mathrm{DO})$$

where R = Oláh respiration coefficient (per hour) and the other variables are as defined for equation 1. For comparison purposes, the same diffusion component used in the WPRD model was employed in the Oláh model. The models only differed in their whole pond respiration components. Oláh et al. (1978) modeled whole pond respiration rate as independent of water temperature.

Water temperature was assumed to decay exponentially during the night in both the WPRD and Oláh models. Regression analysis of water temperature as a function of time (based on data from several different sites in Hawaii) indicated that this assumption was well met. Between 95 and 99.9% of the variation in the dependent variable, i.e. log-transformed water temperature, was explained by time. In applying either the WPRD or Oláh model, the procedure described by Madenjian et al. (1987b) was used to fit the exponential decay function to water temperature observed at dusk and approximately 3 h after dusk.

Sampling Methods

For details on the sampling procedures, see the methods section in Madenjian et al. (1988). All sampling was conducted in marine shrimp (*Penaeus vannamei* and *P. monodon*) ponds on the island of Oahu in Hawaii between July and December 1986. Thirty overnight trials were performed both at Amorient Aquafarm Inc. in Kahuku and at the Mariculture Research and Training Center (MRTC) in Hakipuu (about 10 km north of Kaneohe). During each Amorient trial, DO and water temperature were observed at dusk, approximately 3 h after dusk, and at dawn. DO and water temperature in the MRTC ponds were measured every 10 min throughout the night using an automated data logging system. Additionally, wind speed was monitored at both sites during the night. An estimate of wind speed was used to determine the oxygen transfer coefficient, KL. Strong winds prevented stratification in the Amorient ponds during the study period. Mechanical circulators were deployed in the MRTC ponds to prevent stratification. On the average, water temperature dropped 1.6 and 2.1°, while DO dropped 7.1 and 3.1 mg $O_2 \cdot L^{-1}$, during the night in the MRTC and Amorient ponds, respectively.

TABLE 1. Minimum (Min.), maximum (Max.), and mean plus standard error (SE) of the absolute value of the residuals from fitting the WPRD and Oláh models to data from marine shrimp ponds at Amorient (Kahuku, Oahu) and at MRTC (Hakipuu, Oahu), July through December 1986. The dawn DO predictions of the models were based on observations of DO at dusk and approximately 3 h after dusk. The residual is the observed dawn DO minus the predicted dawn DO. *N* = number of trials.

		Absolute value of residuals (mg $O_2 \cdot L^{-1}$)		
Site	*N*	Min.	Max.	Mean (SE)
		WPRD model		
Amorient	30	0.02	1.00	0.27 (0.04)
MRTC	30	0.05	1.34	0.52 (0.07)
Amorient and MRTC pooled	60	0.02	1.34	0.39 (0.04)
		Oláh model		
Amorient	30	0.07	0.88	0.37 (0.04)
MRTC	30	0.07	2.32	1.16 (0.10)
Amorient and MRTC pooled	60	0.07	2.32	0.77 (0.08)

Application of the Models

Both the WPRD and Oláh models were applied to the same data set composed of 30 overnight trials at each of the Amorient and MRTC sites. The WPRD model was fitted to the observations of DO at dusk and approximately 3 h after dusk in order to estimate the respiration coefficient, c. Then a Runge–Kutta numerical integration routine was used to evaluate the integral of the differential equation (equation 1) between the time limits defining the night to obtain a prediction of dawn DO. By fitting the Oláh model to DO observations at dusk and approximately 3 h following dusk, the Oláh respiration coefficient, R, was estimated. The integral of equation 2 was then evaluated to generate a prediction of dawn DO by the Oláh model.

Descriptive statistics for the absolute value of the residuals (the residual is equal to observed dawn DO minus predicted dawn DO) from the different model applications were calculated and compared. To examine the models for bias, predictions of dawn DO were regressed upon observed dawn DO. For more details on model application, see the model verification section in Madenjian et al. (1988).

Results

The WPRD model was slightly more accurate in its forecasts of dawn DO for Amorient ponds than the Oláh model; but the WPRD model was substantially more accurate than the Oláh model for the MRTC ponds (Table 1). Overall, the mean absolute value of the residuals from the Oláh model (0.77 mg $O_2 \cdot L^{-1}$) was almost twice as great as that for the WPRD model

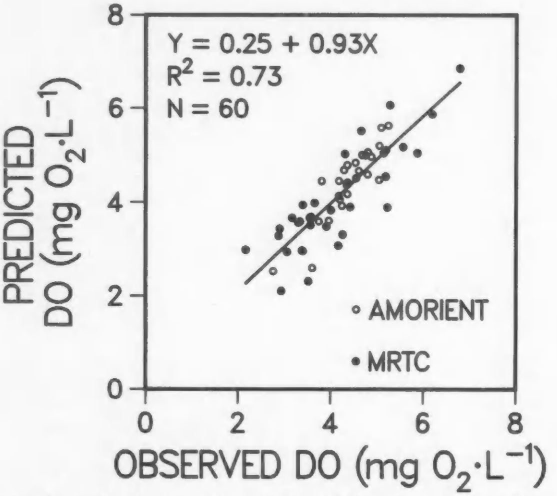

FIG. 1. Predicted versus observed pond DO at dawn for Amorient ponds (Kahuku, Oahu) and MRTC ponds (Hakipuu, Oahu), July through December 1986. Predicted dawn DO was based on the WPRD model using a 3-h lag between the dusk and second DO measurements (taken from Madenjian et al. 1988).

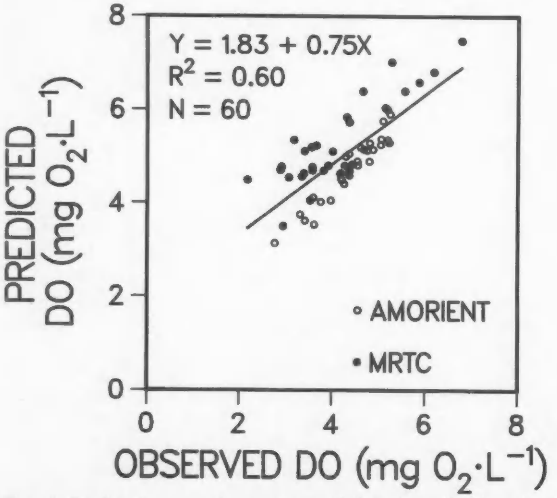

FIG. 2. Predicted versus observed pond DO at dawn for Amorient ponds (Kahuku, Oahu) and MRTC ponds (Hakipuu, Oahu), July through December 1986. Predicted dawn DO was based on the Oláh model using a 3-h lag between the dusk and second DO measurements.

(0.39 mg $O_2 \cdot L^{-1}$) (Table 1). The WPRD model overestimated dawn DO in 31 of 60 trials whereas the Oláh model overestimated dawn DO in 59 of 60 trials. Regression of predicted dawn DO on observed dawn DO revealed that there was no detectable bias in the WPRD model (α was set equal to 0.05 for tests of significance of the regression line parameters) (Fig. 1). Since the slope of the line was not significantly different from unity and the *y*-intercept was not significantly different from zero, there was a 1:1 correspondence between predicted and observed DO at dawn. In contrast, the slope of the regression line for predicted dawn DO on observed dawn DO using the Oláh model was 0.75 (the slope was significantly different from unity, sample *t*-statistic = -3.160, $p = 0.0025$), and the intercept was significantly different from zero (intercept = 1.83, sample *t*-statistic = 5.309, $p < 0.0001$) (Fig. 2). These results indicated considerable bias in the Oláh model predictions.

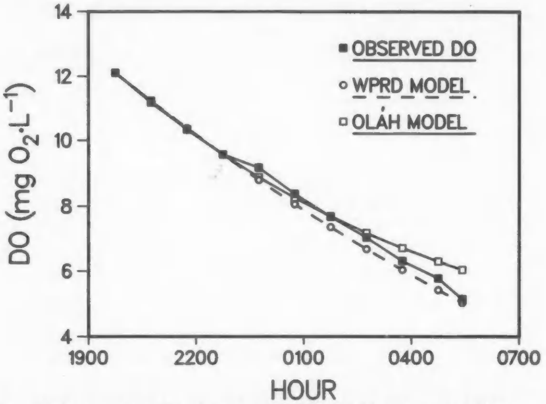

FIG. 3. Observed and predicted pond DO in MRTC pond 7 (Hakipuu, Oahu) during the night beginning on August 30, 1986. Predicted DO was based on the WPRD and Oláh models using DO observations at 1935 and 2235.

This bias is illustrated in a plot of predicted and observed DO for MRTC pond 7 for the night of August 30–31, 1986 (Fig. 3). The WPRD model tracked the observed decline in DO closely during the entire night. The Oláh model predicted pond DO accurately during most of the night. However, towards the end of the night the deviation between the Oláh model prediction and the observed DO increased so that overestimation became more serious with time.

Discussion

The WPRD model proved to be a more accurate forecaster of early morning pond DO than the Oláh model. The substantially greater accuracy of the WPRD model than the Oláh model at the MRTC site, in comparison with the modest difference in accuracy between the two models at Amorient, may be attributed to differences in whole pond respiration rate and wind conditions between the two sites. The Amorient site was considerably windier (average observed nightly wind speed of 8.25 $m \cdot s^{-1}$ during the study opposed to 1.27 $m \cdot s^{-1}$ at MRTC), but the MRTC ponds exhibited higher whole pond respiration rates than the Amorient ponds (Madenjian et al. 1988). Correspondingly, the MRTC ponds showed a greater drop in observed DO during the night than the Amorient ponds. Based on the Oláh model, the decrease in the respiration rate during the night is a function of the observed drop in pond DO. If the respiration rate of the whole pond is independent of DO, then the departure of the Oláh model prediction curve from the observed DO curve is expected to increase as the nighttime drop in pond DO increases.

Evidence from channel catfish (*Ictalurus punctatus*) ponds in Alabama supported the contention that the nighttime pond respiration rate is independent of pond DO (Boyd et al. 1978; Romaire et al. 1978; Romaire 1979). Boyd and Romaire represented pond respiration rate as independent of DO in their models for the overnight pond DO dynamics. Their models have proved to be accurate predictors of early morning DO in catfish ponds. The ponds modeled by Oláh et al. (1978) for a 24-h period may also have exhibited a nighttime respiration rate that was independent of DO. In the Oláh et al. (1978) study, the error introduced by describing nighttime pond respiration rate as DO dependent may have been balanced by error in modeling a DO-dependent daytime respiration rate.

Several laboratory studies have shown that fish and shrimp respiration rates are independent of DO unless DO is below a critical concentration. This critical DO level has been reported to be between 3 and 4 mg $O_2 \cdot L^{-1}$ for grass shrimp (*Penaeus monodon*) (Liao and Murai 1986), about 50% of DO saturation for brook trout (*Salvelinus fontinalis*) (Fry 1971), and about 2 mg $O_2 \cdot L^{-1}$ for tilapia (*Oreochromis niloticus*) (Verheyen et al. 1985). Respiration of the cultivated organisms is usually a minor fraction of total respiration in aquaculture ponds (Boyd et al. 1978; Romaire 1979; Madenjian et al. 1987a; Madenjian 1988). In prawn and shrimp ponds, the water column and pond sediments are the major consumers of oxygen (Madenjian et al. 1987a; Madenjian 1988). Respiration of unicellular aquatic organisms collected in the water column has been described as independent of DO, unless DO is very low (less than 1.0 mg $O_2 \cdot L^{-1}$) (ZoBell 1940). In a review of lake sediment oxygen demand, Walker and Snodgrass (1986) have noted a strong relationship between sediment oxygen uptake and lake DO when DO is below 1 or 2 mg $O_2 \cdot L^{-1}$. However, when DO is greater than 2 mg $O_2 \cdot L^{-1}$, oxygen uptake rate by sediments in lakes, bays, or estuaries has been reported to be independent of DO (Martin and Bella 1971; Es 1982) and dependent on DO (Hargrave 1969; Edberg and Hofsten 1973). The apparent discrepancy in the reported results may be due to varying degrees of chemical oxygen demand in sediments and to employment of different incubation procedures. In the present study, the observed nighttime DO ranged from 2 to 14 mg $O_2 \cdot L^{-1}$, and dawn DO was greater than 3 mg $O_2 \cdot L^{-1}$ in 55 of 60 trials (in the other 5 trials, dawn DO was between 2 and 3 mg $O_2 \cdot L^{-1}$). Hence, the present study supplies evidence that, unless pond DO is very low, nighttime respiration of the most important consumers of oxygen in aquaculture ponds is unaffected by the pond DO level.

In summary, whole pond respiration rate at night was better characterized as dependent on water temperature than on DO. The WPRD model, based on respiration rate as a function of water temperature, yielded more accurate predictions of dawn DO in aquaculture ponds than the Oláh model, in which respiration rate was directly related to DO. Results indicated a bias in the predictions of early morning DO by the Oláh model, such that dawn DO was consistently overestimated.

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A Catch-at-Length Analysis that Incorporates a Stochastic Model of Growth[1]

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Sullivan, P. J., H. L. Lai, and V. F. Gallucci. 1990. A catch-at-length analysis that incorporates a stochastic model of growth. Can. J. Fish. Aquat. Sci. 47: 184–198.

A length-structured population model, which incorporates von Bertalanffy growth, is used to describe changes in population abundance over time. The model is incorporated into a catch-at-length algorithm that uses a nonlinear least squares approach to estimate relative abundance, fishing mortality, selectivity, and the von Bertalanffy growth parameters L_∞ and k. The algorithm is applied to a simulated data set for Pacific cod (*Gadus macrocephalus*) and to catch data on *Pseudotolithus typus* and *Decapterus russellii*. The parameter estimates of Pacific cod obtained from this algorithm were comparable with the values that were originally used to simulate the data. Although the catch data of *P. typus* did not exhibit the full range of sizes present in the population due to differential vulnerability of the population to the fishery, the estimates of L_∞ and k reflect the growth over the entire size range of the population. Other population estimates for *P. typus* were in agreement with observed biological information. The estimated growth parameters L_∞ and k of *D. russellii* showed some discrepancy with the information available on mature individuals present in this fishery but appeared to adequately represent year 1 growth. The estimated population and exploitation parameters fit the observed catch-at-length. Estimates made with the catch-at-length approach can be improved by using auxiliary information that may be available on abundance, fishing effort, recruitment, and growth.

Nous avons utilisé un modèle de population fondé sur la répartition des tailles des poissons qui prend en compte les paramètres de croissance de von Bertalanffy pour décrire les variations de l'abondance d'une population dans le temps. Nous avons intégré ce modèle à un algorithme de prise par longueur qui utilise les moindres carrés de façon non linéaire pour estimer l'abondance, la mortalité due à la pêche et la sélectivité relatives de même que les paramètres de croissance L_∞ et k de von Bertalanffy. L'algorithme a été appliqué à un ensemble de données simulées relatives à la morue du Pacifique (*Gadus macrocephalus*) et à des données de capture relatives à *Pseudotolithus typus* et *Decapterus russellii*. Les valeurs estimées des paramètres pour la morue du Pacifique obtenues grâce à cet algorithme étaient comparables à celles qui ont été utilisées originalement pour simuler les données. Même si les données de capture de *P. typus* ne couvraient pas l'ensemble de la fourchette de taille de la population, à cause de la plus ou moins grande vulnérabilité des poissons à la pêche selon leur taille, les estimations de L_∞ et k étaient représentatives de la croissance pour l'ensemble des classes de taille de la population. D'autres estimations de population pour *P. typus* correspondaient à certaines données biologiques disponibles. Les paramètres de croissance estimée L_∞ et k pour *D. russellii* ont montré un écart par rapport aux informations disponibles sur les individus matures du stock de pêche, mais ils semblaient valables pour la première année de croissance des poissons. L'estimation de la population et les paramètres d'exploitation correspondaient avec les prises par longueur. Les estimations effectuées avec cette méthode des prises par longueur peuvent être améliorées si l'on utilise des informations supplémentaires éventuellement disponibles relatives à l'abondance, à l'effort de pêche, au recrutement et à la croissance.

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The estimation of stock abundance, recruitment, fishing mortality, and gear selectivity is the principal objective of stock assessment. Many of the principal contemporary estimation procedures are based on the application of the Baranov catch equation (Ricker 1975) to catch data classified by age group. This has led to the development of several powerful stock assessment algorithms including virtual population analysis or VPA (Fry 1949; Gulland 1965; Murphy 1965), cohort analysis (Pope 1972); and catch-at-age analysis (Doubleday 1976; Fournier and Archibald 1982; Schnute 1985; Deriso et al. 1985). The classification of catch data into strata or groups that are homogeneous by age suggests that higher quality inferences (Quinn 1986) will result, but there are associated high costs. The determination of age may be hampered by inaccuracy, imprecision, or a lack of valid ageing methods (Lai 1985). These difficulties are partially resolved by the use of an estimation procedure based on the *length* composition of the catch.

Many length-based stock assessment methodologies depend on a von Bertalanffy growth model to translate length into age so that the exponential decay cohort model can be applied. Length–cohort analysis (Jones 1979, 1984; Lai and Gallucci 1987, 1988) and estimators of Z/k (e.g. Beverton and Holt 1956; Ssentongo and Larkin 1973) are among the most popular. However, a number of assumptions fundamental to these length-based methods limit their applicability: (1) length distributions are in a steady state over time, (2) recruitment to the fishery is knife-edged and constant, and (3) growth is a deterministic process with length-at-age being well defined. The stock assessment estimation methodology developed in this paper makes no assumptions about the steady state of length distributions and the knife-edged constant recruitment; it computes gear selectivity as a function of fish length from the data, and it describes growth with a stochastic model based on the probability of individuals moving from one length category to another.

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The input is catch data in the form of a time series of length distributions and a set of starting values to initiate the optimization algorithm. The output is a set of estimates of abundance and recruitment over length at specific times, fishing mortality over time, gear selectivity by fish length, as well as estimates of the growth parameters L_∞ and k from the von Bertalanffy model.

Model Development

The model that underlies this estimation procedure characterizes the dynamics of the population in terms of numbers at length over time. This length-structured mathematical model describes the exploitation and growth of individuals in the population explicitly in terms of length and is formulated in terms of two basic relationships. The first relates catch-at-length to abundance. The second characterizes changes in numbers at length from one time step to the next.

Catch ($C_{l,t}$) for a given length class l ($l = 1, \ldots, n$) and time t ($t = 0, \ldots, t_{\max}$) is related to the number of individuals in the population ($N_{l,t}$) in that length class at that time through a length-based exploitation rate ($\mu_{l,t}$). The general form of the Baranov catch equation (Ricker 1975) indexed in terms of length class rather than age, holds at time t for fish of length class l:

$$(1)\quad C_{l,t} = \mu_{l,t} N_{l,t}$$

where the exploitation rate $\mu_{l,t}$ represents the proportion of individuals that die due to fishing mortality, given they were in length class l at time t. The exploitation rate is therefore dependent on the fishing mortality rate $F_{l,t}$ and total mortality rate $Z_{l,t}$ of fish of length class l during time t in the following way:

$$(2)\quad \mu_{l,t} = \frac{F_{l,t}}{Z_{l,t}}(1 - e^{-Z_{l,t}})$$

where $F_{l,t}$ and $Z_{l,t}$ are in units of $1/\Delta t$. Combined, equations (1) and (2) reflect the standard form of the Baranov catch equation with individuals classified by length rather than age. The units of the time interval Δt may be expressed in years, as they are in most age-structured models, but they may also be expressed in terms of the time increment over which the observations were collected (e.g. months, weeks, etc.), which may also change from time step to time step.

Fishing mortality is a function of fishing effort and gear selectivity. We assume that fishing mortality is separable into a product of a length-specific selectivity coefficient s_l and a full-recruitment fishing mortality rate f_t at time t following Doubleday's (1976) approach for age-based groups and express it as

$$(3)\quad F_{l,t} = s_l f_t.$$

The length-specific selectivity coefficient s_l is interpreted as the fraction of fish in length class l subjected to the full effect of fishing mortality. It is represented by a gamma-type function:

$$(4a)\quad s_l = \frac{l^{\alpha_s} e^{-\beta_s l}}{\max_k (k^{\alpha_s} e^{-\beta_s k}}$$

or a logistic function:

$$(4b)\quad s_l = \frac{1}{1 + \alpha_s e^{-\beta_s l}}$$

where s_l is rescaled such that the largest s_l is set to 1 to ensure that fishing mortality rates are well defined. The first function is modified from an age-structured formulation suggested by Deriso et al. (1985) and is flexible enough to allow many realistic shapes for the selectivity curve, while the second function is more conventional and probably easier to use. In fact, these two relationships are very easy to apply and constrain. For example, in gamma-type functions, if the length class k where $s_k = 1$ is known, then $k = \alpha_s/\beta_s$ or $\alpha_s = \beta_s k$. The estimated parameters can further be reduced. Logistic curves also can be constrained in the length class l when $s_l = 0.5$ is known.

The total instantaneous mortality of individuals in length class l at time t is separable as the sum of the instantaneous fishing and natural mortality rates:

$$(5)\quad \begin{aligned} Z_{l,t} &= F_{l,t} + M_{l,t} \\ &= s_l f_t + M_{l,t}. \end{aligned}$$

The relationship between the number of individuals ($N_{l,t}$) at time t and the number ($N_{l,t'}$) present at a later time t' is described in terms of the numbers of fish at length surviving and growing into the next time period. If growth is negligible for fish initially in length class l, at time t, then the total number of fish in length class l surviving to the start of time period t' is reduced only by mortality:

$$(6)\quad N_{l,t'} = N_{l,t} e^{-Z_{l,t}}$$

for each length class l ($l = 1, \ldots, n$).

To account for growth, a model is incorporated that combines the inherent variability seen in individual growth with the general nonlinear trend frequently observed for the population as a whole. Growth is represented by the proportion $P_{l,l'}$ of surviving individuals in length class l during a fixed time interval. The proportion $P_{l,l'}$ of individuals that grow from a length class l to all length classes l' ($l' = l, \ldots, n$) is assumed to be represented by a probability distribution function that can be parameterized by its mean and its variance. The mean represents the average growth increment which then can be described by any standard deterministic growth model. The variance represents the individual variability in growth, which in many circumstances is proportional to the mean (Schnute and Fournier 1980; Fournier and Breen 1983); together, under such a formulation, the mean and variance uniquely determine the proportion of individuals going from one length class to another.

For example, to represent the mean of the distribution, consider growth following the von Bertalanffy model:

$$(7)\quad L_t = L_\infty (1 - e^{-k(t - t_0)})$$

where L_t is the length of an individual at age t, t_0 is the time correction factor for the size at birth or recruitment, L_∞ is the theoretical asymptotic length of an individual, and k is the Brody growth constant. Based on this model, the growth increment Δ_l

over a unit time interval $(t, t+1)$ for a fish starting at length class l at time t with length of L_t can be described as (Chapman 1960)

$$(8) \quad \Delta_l = L_{t+1} - L_t$$

that may vary from individual to individual. By fixing L_t at the midlength (l_*) of the length class l, Δ_l represents the change in length of an individual initially in length class l. The mean growth increment $\bar{\Delta}_l$ for the individuals in length class l is then the average change in length of individuals initially in length class l:

$$(9) \quad \bar{\Delta}_l = (L_\infty - l_*)\,(1 - e^{-k}),$$

an expression that is independent of t_0.

By differencing, as in equation (8), the need for interpretation of time as age in equation (9) is eliminated. Other growth models could be used but the von Bertalanffy growth model offers the most in terms of comparative opportunities in the literature.

For this work, a gamma distribution was used to represent the variation in growth described as above. The gamma distribution was chosen for its versatility and flexibility in approximating several functional forms. It is also definable entirely in terms of its first and second moments, thus reducing the number of parameters to be estimated. Flexibility is required to describe the different patterns of growth for small and large fish. Smaller fish grow faster and the distribution of the change in length Δ_l may be slightly skewed positively. Larger fish grow more slowly, which tends to restrict the growth to adjoining length categories, and the distribution of Δ_l is more concentrated about the mean.

The gamma distribution expressed in terms of the parameters α_l and β (Hogg and Craig 1970) is

$$(10) \quad g(x|\alpha_l,\beta) = \frac{1}{\beta^{\alpha_l}\Gamma(\alpha_l)}\, x^{\alpha_l - 1} e^{-x/\beta}$$

where x represents Δ_l (the growth increment, given a fish was originally in lengthclass l). The mean change in length is given by $\bar{\Delta}_l = \alpha_l\beta$ and the variance is given by $\sigma_l^2 = \alpha_l\beta^2 = \beta\bar{\Delta}_l$ which is proportional to the mean, as required. In this expression, β is also the coefficient of variation which is used to incorporate the growth variability of individuals in the population. Given l_* and β, the parameters α_l, and consequently $\bar{\Delta}_l$ and σ_l^2, are functions of the two von Bertalanffy parameters L_∞ and k.

The catch observations are classified into length classes, and the growth of individuals in a length class, say class l, where the length of these individuals may range in length from l_1 to l_2 is approximated by the growth of a midlength individual ($l_* = (l_1 + l_2)/2$) of the class. The expected proportion of individuals growing from length class l to length class l' can then be found by integrating over the length range (l'_1, l'_2) of the receiving length class l' at the beginning of the next time period t':

$$(11) \quad P_{l,l'} = \int_{l'_1}^{l'_2} g(x|\alpha_l,\beta)\,dx.$$

Any fish that enters into a length class with the midlength greater than L_∞ is assumed to remain in the class subject to survivorship (i.e. $P_{l',l'} = 1$ for $l' \geq L_\infty$).

A similar model for growth was developed by Gutreuter and Anderson (1985) in describing the effect of body size on recruitment in largemouth bass (*Micropterus salmoides*) populations. They noted that a gamma distribution function usefully incorporates a variance in the change in length that increases as a function of the change in length. DeAngelis and Coutant (1979) used a partial differential equation growth model and showed that the variance about mean length increases, perhaps quadratically, as a function of time. The von Bertalanffy model, used as above, constrains the number of parameters needed to describe growth to three parameters, L_∞, k, and β, while allowing a stochastic description of growth.

Equations (6) through (11) are now used to calculate the total number of fish $N_{l',t'}$ of lengthclass l' at the start of the next time step t' as

$$(12) \quad N_{l',t'} = \sum_{l} P_{l,l'} N_{l,t} e^{-Z_{l,t}}.$$

In this formulation, growth is time (age) invariant. The model can be modified to allow for functional dependence to represent more complex growth patterns.

To complete the description of the dynamics, a renewal function which includes recruitment to the fishery is added to equation (12):

$$(13) \quad N_{l',t'} = \sum_{l} P_{l,l'} N_{l,t} e^{-Z_{l,t}} + R_{l',t'}$$

where recruitment to the fishery may occur over a range of length classes. Recruitment specified in this way more generally represents the type of recruitment observed in nature where variation in growth, behavior, or food supply can result in individuals entering the main body of the population at various sizes. Length-specific selectivity (s_l) is then combined with recruitment to the population to reflect the effective entry of individuals to the catch (Gulland 1969). There are several ways of representing recruitment to length class categories beyond the first length class. For example, recruitment to each length class might be represented by a series of constant values $\{R_{l,t}: l = 1, \ldots, n\}$ for each time step t. In the estimation procedure outlined below, however, recruitment is separated into a time-dependent variable R_t and a length-dependent variable p_l, representing the proportion of recruits going to each length class:

$$(14) \quad R_{l,t} = R_t p_l.$$

One advantage of separating variables is that R_t can be compared with recruitment estimates from standard procedures, such as recruitment to the first age class, while the proportion of recruits going into length classes $\{l: l = 1, \ldots, n\}$ may be represented by another two-parameter gamma distribution, such as the one shown in equation (10), with recruitment parameters α_r and β_r.

The model (13) describes a linear transition of the number of individuals in length class l at time t to the numbers in length class l' at time t'. This model may also be written in matrix notation:

$$(15) \quad \begin{bmatrix} N_{1,t'} \\ N_{2,t'} \\ \vdots \\ N_{l',t'} \\ \vdots \\ N_{n,t'} \end{bmatrix} = \begin{bmatrix} P_{1,2} & 0 & & & & 0 \\ P_{1,2} & P_{2,2} & & & & \\ & & * & & & \\ & & & P_{l,l} & & \\ & & & & * & 0 \\ P_{1,n} & P_{2,n} & & & P_{n-1,n} & P_{nn} \end{bmatrix}$$

$$\times \begin{bmatrix} S_{1,t} & 0 & & & & 0 \\ 0 & S_{2,t} & & & & \\ & & * & & & \\ & & & S_{l,l} & & \\ & & & & * & 0 \\ 0 & & & & 0 & S_{n,t} \end{bmatrix} \begin{bmatrix} N_{n,t} \\ N_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ N_{n,t} \end{bmatrix} + \begin{bmatrix} R_{1,t} \\ R_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ R_{n,t} \end{bmatrix} + \begin{bmatrix} w_{1,t} \\ w_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ w_{a,t} \end{bmatrix}$$

with $S_{l,t}$ now representing the exponential survivorship, $e^{-Z_{l,t}}$, term in equation (6). Note that Sainsbury (1982) used a length-based transition matrix similar in form to equation (15) to study the pattern of recruitment in a yield-per-recruit analysis and addressed the implications minimum size limits have on yield and yield-per-recruit.

Equation (1) can also be expressed in matrix form:

$$(16) \quad \begin{bmatrix} C_{1,t} \\ C_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ C_{n,t} \end{bmatrix} = \begin{bmatrix} \mu_{1,t} & 0 & & & & 0 \\ 0 & \mu_{2,t} & & & & \\ & & * & & & \\ & & & \mu_{l,t} & & \\ & & & & * & 0 \\ 0 & & & & 0 & \mu_{n,t} \end{bmatrix} \begin{bmatrix} N_{n,t} \\ N_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ N_{n,t} \end{bmatrix} + \begin{bmatrix} v_{1,t} \\ v_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ v_{n,t} \end{bmatrix}.$$

Time-dependent error vectors $\mathbf{w}_t$ and $\mathbf{v}_t$ are included in equations (15) and (16), respectively, to make the derivation complete and to reflect the stochastic nature of the real population.

Note that the standard age-structured model is a special case of the above, with the subdiagonal probabilities of the length transition matrix P in equation (15) equal to 1 and all other elements 0.

Estimation

The model depicted in equations (15) and (16) is a linear dynamic system and falls into a family of state space models frequently used by engineers, economists, and statisticians (Akaike 1974a, 1974b; Harvey 1981; Priestley 1981; Aoki 1987). If the error vectors $\mathbf{w}_t$ and $\mathbf{v}_t$ can be assumed to be multivariate Gaussian, then the analysis follows directly from the state space Kalman filter methodology (Kalman 1960; Kalman and Bucy 1961).

Under the assumption of no system error ($\mathbf{w}_t \equiv \mathbf{0}$) in equation (15), which means that (i) an exact proportion of individuals go from one length category to the successive ones and (ii) survivorship and recruitment operate deterministically, and with the additional assumption that error ($\mathbf{v}_t$) in the catch equation (16) is independently and identically distributed, the model parameters may be estimated using a nonlinear least squares approach to minimize the resdiual sum of squares:

$$(17) \quad \mathrm{RSS}_{\mathrm{catch}} = \sum_{l,t} (C'_{l,t} - C_{l,t})^2$$

where $C'_{l,t}$ is the predicted catch-at-length and $C_{l,t}$ is the observed catch-at-length at time t.

The observed data are catch in number over a set of specified length classes, taken over equally spaced time intervals. The observations of catch $C_{l,t}$ in number in length classes $l = 1, \ldots, n$ at times $t = 0, \ldots, t_{\max}$ are used to estimate the population parameters defined above. The parameters to be estimated are the parameters α_s and β_s for selectivity functions, full recruitment fishing mortality f_t, initial population numbers at length $N_{l,0}$ ($l = 1, \ldots, n$), recruitment to the fishery R_t over time $t = 1, \ldots, t_{\max}$, the recruitment distribution parameters α_r and β_r, and the growth parameters L_∞ k, and β.

In practice, if any parameters happen to be known, these known parameters can be fixed in estimation. However, if some parameters can be obtained from additional observation (e.g. when the fishing efforts are known), then they can be used as auxiliary data. In this example, a functional relationship

$$f_t = qE_t$$

is used, where q is catchability to be estimated and assumed constant over time and E_t is observed fishing effort at time t. Then the residual sum of squares to be minimized becomes

$$\mathrm{RSS} = \sum_{l,t} (C'_{l,t} - C_{l,t})^2 + \lambda \sum (f'_t - f_t)^2$$

where λ is the weight that describes the degree of confidence in the effort estimates. Other auxiliary data, such as hydroacoustic estimation of population size at any time, mean length-at-age from age determination, and survey data on recruitment, can also be included in the same manner without difficulty.

When it is valid to assume that the elements of the observation error vector $\mathbf{v}_t$ are independent identically distributed Gaussian random variables, that is, when

$$\mathbf{v}_t \sim N(\mathbf{0}, \sigma^2\mathbf{I})$$

where $\mathbf{0}$ is a vector of zeros, σ^2 is a constant variance, and $\mathbf{I}$ is the identity matrix (a diagonal matrix of ones), then the solution to the least squares fit is also the maximum likelihood solution (Seber 1977). Other assumptions about the system equation and the catch equation error structure may be made that can result in more complicated and sometimes more reasonable forms of the least squares formulation (e.g. a weighted least squares formulation).

A Marquardt–Levenberg optimization algorithm is used to find the least squares estimates of the model parameters. The optimization routines require that initial estimates of the unknown parameters be supplied. There is some sensitivity to those initial parameter estimates due to local minima in the sum of squares function. Initial value sensitivity can be investigated by using an array of initial estimates (Sullivan 1988; Lai and Gallucci 1989). In the analyses to follow, the initial estimates are arrived at from the available literature. In some instances, certain parameters are assumed to be fixed and known in order for the parameter space to be well defined.

In the estimation procedure, only the values of $N_{l,0}$ need be estimated. The values of $N_{l,t}$ for $t = 1, \ldots, t_{\max}$ can be computed recursively from $N_{l,t-1}$, the abundance at the preceding time steps using equation (15). To simplify the parameter space even further, $N_{l,0}$ is calculated from the total initial population abundance N_0 (where $N_0 = \Sigma_l N_{l,0}$) using the frequency distribution of the initial catch-at-length ($C_{l,0}$) and length-specific fishing mortalities estimated by the algorithm. This procedure is presented further in Appendix 1.

Model Application and Analysis

The model was applied to one simulated data set and two commercial fishery data sets. The simulated data set was generated to describe the dynamics of Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea. One set of data was collected from commercial catch of *Pseudotolithus typus* from the Cameroon coast (Djama 1988) and the other is based on market survey data from the commercial catch of *Decapterus russellii* from the Java Sea, Indonesia (Widodo 1988). The simulated data set is presented to highlight certain features of the estimation procedure as it applies to a set of observations for which

TABLE 1. Parameter values used in the simulation.

Parameter	Value
Number of age classes	12
Abundance at:	
Age 1	1.10×10^9
Age 2	2.14×10^8
Age 3	1.20×10^7
Age 4	1.10×10^7
Age 5	6.00×10^6
Age 6	6.00×10^6
Age 7	2.10×10^6
Age 8	1.00×10^6
Age 9	1.00×10^6
Age 10	1.00×10^6
Age 11	1.00×10^6
Age 12	1.00×10^6
N_0	1.36×10^9
Number of time steps (years)	10
Number of length classes	45
α_r	37.00
β_r	0.50
R_1	4.42×10^8
R_2	1.32×10^8
R_3	1.39×10^8
R_4	8.60×10^7
R_5	9.00×10^7
R_6	1.65×10^8
R_7	1.05×10^8
R_8	1.28×10^8
R_9	9.70×10^7
M	0.30
α_s	0.10
β_s	30.00
f_0	0.42
f_1	0.44
f_2	0.46
f_3	0.48
f_4	0.47
f_5	0.48
f_6	0.45
f_7	0.48
f_8	0.40
f_9	0.43
L_∞	83.00
κ	0.24
β	1.0

the underlying system structure and the underlying process parameters are known a priori. The second two analyses demonstrate the applicability of this approach in the context of actual fishery data.

Gadus macrocephalus Simulation

For initial validation of the estimation procedure, a hypothetical data set was created using a computer-simulated model based on equations (1) and (13). Parameter values representing the initial population size, growth, recruitment, natural and fishing mortality, and selectivity were chosen to reflect the dynamics exhibited by Pacific cod in the eastern Bering Sea. The parameter values were set equal to actual estimates arrived at by Bakkala and Low (1985), so that the model dynamics would be representative of observations from the natural system. The initial population was based on the survey estimates of population number at ages (Bakkala and Low 1985) and transformed into forty-five 2-cm-wide length classes using an age–length key (Lai 1985). The simulation depicts population numbers and catch numbers in terms of forty-five 2-cm-wide length classes and 10 time intervals, each a year in duration. Fishing mortality was allowed to differ from one year to the next, while selectivity was assumed to be a logistic function (4b). The growth increment Δ_l was calculated for each length class l by using the values of L_∞ and k given in Lai (1985), while β was set equal to 1, indicating a variance in growth that is equal to the mean. The recruitment distribution was set equal to the observed length distribution of age 1 individuals given for the first year (1978) of the time series in Bakkala and Low (1985). Independently distributed Gaussian error, with variance equal to 10^5 times the average number of individuals observed in a catch–length class, was added to the observations to simulate the observation error $\mathbf{v}_t$. In this example, the constant of proportionality reflects a coefficient of variation of approximately 0.2. A summary of the parameters used in the simulation is given in Table 1.

The simulated data set is characterized by an influx of the strong 1977 year class in the first year (1978) that grows and declines, giving way in influence in subsequent years to the stronger influence of recruitment (see Fig. 1). For the first estimation with the simulated data, the initial values of all parameters were set to true values (Table 2). In the second estimation, the initial values of all parameters were randomly set to ±30% of the true values (Table 2). All parameters except natural mortality (M) were subject to estimation in these two cases.

Figure 1 compares the estimated catch values with the catch values from a simulation where the input values were varied ±30% from the (known) true values. In both estimations, the parameters estimated (Table 2) show good correspondence within known values, although some difference in the recruitment estimates can be seen over later time periods. Here, as in catch-at-age analysis (Deriso et al. 1985; Kimura 1989), auxiliary information may prove useful in obtaining better estimates. Note, however, that even with deviations of ±30%, the estimation algorithm appeared to be robust.

Pseudotolithus typus

In order to ascertain the applicability of this approach under more realistic circumstances, two fisheries data sets were selected from existing literature. The first set of data is the 1984 monthly length–frequency distributions (February – November) of longneck croaker (*Pseudotolithus typus*: Sciaenidae) collected from commercial fisheries in Cameroon (Djama 1988). This species is one of two major finfish species caught by industrial trawl fisheries at depths between 10 and 50 m off the Cameroon coast. Five companies conducted industrial fishing during that period, and data were collected from two of these companies. The data are considered to be representative of the length–frequency distribution of all landings. The procedures used to estimate the catch-at-length for each month were described by Djama (1988).

The observed catch-at-length data are grouped into 1-cm 48 length classes with midlengths ranging from 10.5 to 57.5 cm. No information was available for April, so a single time step of twice Δt was used between March and May. Although information on natural mortality (M) was not available, Djama (1988) was able to obtain estimates of $L_\infty = 83$ cm, $k = 0.025 \cdot \mathrm{yr}^{-1}$, and $Z/k = 8.53$ by using Wetherall's method

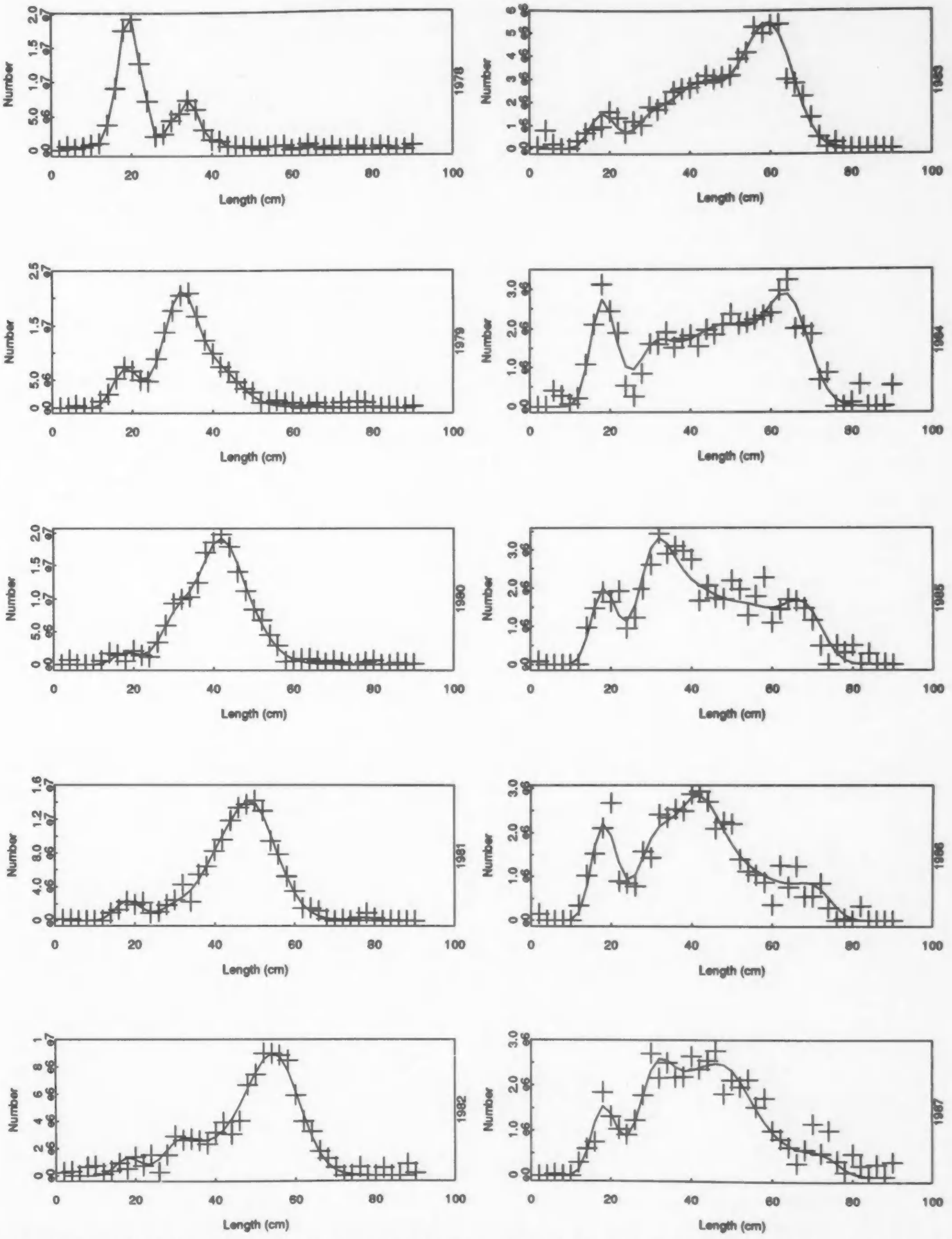

FIG. 1. Simulated (+) and estimated (solid line) catch-at-length data of Pacific cod over 10 consecutive time periods. Simulated catches were generated for a Pacific cod population during 1978–87. Catch estimates were obtained from the catch-at-length least squares algorithm, using initial parameter values which varied ±30% from the true value.

TABLE 2. Simulated and estimated parameter values for Pacific cod.

		Estimate 1		Estimate 2	
	True	Initial (set equal to true values)	Estimated	Initial (set to ±30% of true values)	Estimated
N_0	1.36×10^9	1.36×10^9	1.39×10^9	1.00×10^9	1.39×10^9
α_r	37.0	37.0	30.4	25.0	30.4
β_r	0.5	0.5	0.56	0.7	0.56
R_1	4.42×10^8	4.42×10^8	4.13×10^8	5.75×10^8	4.12×10^8
R_2	1.32×10^8	1.32×10^8	1.16×10^8	9.30×10^7	1.16×10^8
R_3	1.39×10^8	1.39×10^8	1.50×10^8	1.81×10^8	1.50×10^8
R_4	8.60×10^7	8.60×10^7	8.76×10^7	1.06×10^8	8.75×10^7
R_5	9.00×10^7	9.00×10^7	9.85×10^7	6.30×10^7	9.81×10^7
R_6	1.65×10^8	1.65×10^8	1.94×10^8	1.15×10^8	1.93×10^8
R_7	1.05×10^8	1.05×10^8	1.40×10^8	1.50×10^8	1.39×10^8
R_8	1.28×10^8	1.28×10^8	1.89×10^8	9.00×10^7	1.87×10^8
R_9	9.70×10^7	9.70×10^7	1.42×10^8	1.06×10^8	1.41×10^8
α_s	0.1	0.1	0.1	0.3	0.1
β_s	30.0	30.0	32.5	20.0	32.5
f_0	0.42	0.42	0.51	0.3	0.51
f_1	0.44	0.44	0.52	0.6	0.52
f_2	0.46	0.46	0.52	0.3	0.52
f_3	0.48	0.48	0.51	0.65	0.51
f_4	0.47	0.47	0.50	0.25	0.50
f_5	0.48	0.48	0.51	0.60	0.51
f_6	0.45	0.45	0.46	0.70	0.46
f_7	0.48	0.48	0.46	0.30	0.46
f_8	0.40	0.40	0.38	0.60	0.38
f_9	0.43	0.43	0.35	0.30	0.35
L_∞	83.0	83.0	86.1	95.0	86.1
κ	0.24	0.24	0.23	0.30	0.23
β	1.0	1.0	1.04	1.40	1.04

(Wetherall 1986) and $L_\infty = 60$ cm and $k = 0.1 \cdot \text{yr}^{-1}$ by using ELEFAN (Pauly and David 1981). According to the estimates by Wetherall's method, the resulting estimate of total mortality is $Z = 2.14 \cdot \text{yr}^{-1}$, suggesting a natural mortality of around $1.0 \cdot \text{yr}^{-1}$. However, initial runs of the algorithm indicated that the value for M might be too high (i.e. the resulting total instantaneous fishing mortalities were too low, less than $0.0001 \cdot \text{yr}^{-1}$). As a result, the value of M was set equal to $0.6 \cdot \text{yr}^{-1}$ (or $0.05 \cdot \text{mo}^{-1}$), and selectivity was assumed to be a logistic function. The proportionality constant β in the growth equation was evaluated for its influence on predicted growth. The larger the value of β, the wider the distribution of the growth increment Δ_l. To demonstrate the effect of alternative choices of β on the resulting estimates, results are presented for three applications of the algorithm: (i) β fixed at 0.5, (ii) β fixed at 1.0, and (iii) β variable and its value determined by application of the algorithm.

Table 3 lists the results from the three applications of the algorithm. The results show that α_r, β_r, α_s, and β_s did not change substantially from one application to the next. All three runs indicated that all sizes of fish were fully vulnerable to the gear. Djama (1988) reported that the industrial fishery used trawl net gear with stretch mesh sizes ranging from 30 to 40 mm in the cod end, which is capable of retaining all fish larger than 10 cm. The third application of the algorithm estimated β to be 2.14, which is considered too large and results in too wide a spread of the growth increment Δ_l as shown in Fig. 2. Figure 2 indicates that more than 40% of the fish in the 10-cm length class can grow more than 4 cm in a 1-mo period when $\beta = 2.14$, while $\beta = 0.5$ and 1.0 give more reasonable results. This conclusion is also supported by examination of the other estimated parameters (see Table 3). Values of L_∞ were 100.17, 102.46, and 50.18 cm, corresponding to β's of 0.5, 1.0, and 2.14, respectively, and were obtained by the three applications of the estimation procedure. These estimates can be compared with the maximum length of 118 cm observed in the 1984 catch as reported by Djama (1988). Since there were 242 fish with lengths greater than 60 cm in the 1984 catch, which were omitted from the reported catch-at-length data by Djama (1988), the third estimate of $L_\infty = 50.18$ cm seems unrealistic. Also, Bayagbona (1969), using age determination data, obtained an estimate of $L_\infty = 103$ cm and $k = 0.29 \cdot \text{yr}^{-1}$ for the same species in Nigeria. Figure 3 shows the fit of the growth curve, with $L_\infty = 100.17$ cm and $k = 0.029 \cdot \text{mo}^{-1}$, resulting from an estimation with $\beta = 0.5$, to the observations.

Djama (1988) reported that this stock exhibits continuous recruitment; however, with $\beta = 1.0$, recruitment was estimated to occur only in June, August, October, and November, while with $\beta = 0.5$, recruitment was estimated to occur in May and July as well. Figure 4 compares the observed and estimated catch-at-length data. The first modes of all distributions were consistently matched up between the observed and the estimated catches. Recruitment in March and September was expected to be minimal due to the high levels of recruitment taking place in the previous months. The mean length of recruitment is at 19.5 cm which corresponds to length class 10. Figure 4 shows that the peaks of the first component in March and September are at length class 12 (with $l_* = 21.5$ cm) and with a small number of individuals in length classes 0–11. This indicates that the two peaks of the first component in these two

TABLE 3. Parameter estimates of *Pseudotolithus typus* (f, M, and k are in mo^{-1}).

Parameter	Estimate 1	Estimate 2	Estimate 3
N_0	1.98×10^8	3.66×10^8	1.26×10^8
α_r	48.7	48.7	43.8
β_r	0.40	0.40	0.45
R_1	0	0	0
R_2	4.90×10^7	0	0
R_3	9.81×10^7	0	4.90×10^6
R_4	2.50×10^7	0	0
R_5	2.76×10^7	3.06×10^8	1.19×10^7
R_6	0	0	0
R_7	3.45×10^8	2.08×10^8	1.35×10^7
R_8	4.80×10^9	4.07×10^8	3.27×10^8
α_s	1.0	1.0	1.0
β_s	0.001	0.001	0.001
f_0	0.060	0.032	0.098
f_1	0.028	0.030	0.105
f_2[a]	0.066	0.038	0.161
f_3	0.042	0.037	0.107
f_4	0.034	0.034	0.107
f_5	0.026	0.026	0.074
f_6	0.012	0.012	0.037
f_7	0.020	0.023	0.058
f_8	0.003	0.004	0.005
L_∞	100.17	102.46	50.18
k	0.029	0.020	0.093
β	0.5[b]	1.0[b]	2.144
M	0.05[b]	0.05[b]	0.05[b]
RSS	5.1×10^6	7.4×10^6	5.3×10^6

[a] f_2 in 2-mo intervals.

[b] Parameters fixed during the estimation procedure.

months are mainly the results of growth rather than the influx of recruitment. The recruitment in November was particularly strong, as was also reported by Djama (1988). This estimation of recruitment pattern is also similar to the fluctuation of proportion of the first components in each month reported in Djama (1988). Fishing mortality estimates ranged from a high of $0.066 \cdot \text{mo}^{-1}$ ($0.792 \cdot \text{yr}^{-1}$) in May to a low of $0.003 \cdot \text{mo}^{-1}$ ($0.036 \cdot \text{yr}^{-1}$) in November. This corresponds to total mortality rate estimates that range from $1.392 \cdot \text{yr}^{-1}$ in May to $0.636 \cdot \text{yr}^{-1}$ in November during a 1-mo period. The low fishing mortality rate estimated for November is likely due to a reduced number of large fish in the catch coupled with the strong recruitment.

Decapterus russellii

The second of the two fisheries data sets to be examined is based on length composition data collected in 1986 from commercial market landing of the species *Decapterus russellii* from the Karimun, one of the five fishing grounds in the Java Sea, over monthly intervals from May to December, a subset of the data analyzed by Widodo (1988). The catch-at-length observations are classified into twenty-eight 0.5-cm-wide length categories with midlengths ranging from 7.0 to 20.5 cm.

This species has been the major target of purse seine fisheries operating in the Java Sea, Indonesia (Widodo 1988). The annual catch of this species represents roughly 30–40% of the total combined landings in biomass for all commercial fish species caught in the Java Sea. The total monthly commercial catch was known and assumed to have the same length distribution observed in the length–frequency samples. A length–weight relationshp was used to determine the average weight of fish in each of the monthly samples. This average weight was divided into the total biomass of the catch for each month to obtain the total number of fish caught per month. The fish catch in number was then distributed among length classes according to the length–frequency distribution observed for each month in the market sample. Fishing mortality was allowed to vary with time, while selectivity was constrained to be equal to 1 for length classes 14–20 (corresponding to fish lengths ranging from 13.5 to 16.5 cm). Natural mortality was set equal to $0.08 \cdot \text{mo}^{-1}$ ($0.92 \cdot \text{yr}^{-1}$), the middle of the range of estimates of natural mortality ($0.65 - 1.19 \text{ yr}^{-1}$) obtained by Widodo (1988).

In the May observations, two distinct length–frequency distributions were evident. We chose to include only the first distribution, over the 10 length classes ranging from 7.0 to 11.5 cm, because those individuals greater than 11.5 cm, which made up the second distribution, appeared to contribute little to the subsequent catch. The data are therefore interpreted to represent the dynamics of the incoming recruits to this fishery.

For this example, a range of discrete values for β was used in the estimation and the best set of estimates were chosen based on a sum of squares criterion. The results of three of these estimations (with $\beta = 0.25, 0.35,$ and 0.45) are shown in Table 4. Over the range of values chosen, $\beta = 0.35$ resulted in the minimum sum of squares. Figure 5 shows the catch observations in comparison with the catch estimates obtained from the catch-at-length estimation procedure under this set of parameter estimates. The initial length–frequency distribution of individuals shown in the first time period (May) depicts a population of smaller individuals entering the fishery. The drop-off in the number of individuals occurring over smaller length classes in July is interpreted by the algorithm to reflect an influx of new recruits into the population in July, followed by growth into the main body of the population in the ensuing months, and its magnitude is reflected in the recruitment estimate. The recruitment distribution parameters, estimated by the algorithm and shown in Table 4 for $\beta = 0.35$, reflect a mean length of recruitment (4.4 cm), occurring around the eighth length class with a variance of 2.2 cm^2 corresponding to a standard deviation across about 1.5 length classes. The recruitment to the fishery in other months is negligible. The parameters estimated by the algorithm create a model fit that reflects the recruitment and growth of recruits as well as the survival and growth of the body of larger individuals. Again, the fishing mortality parameters appear to be fairly consistent in magnitude over time with the exception of the first time period, suggesting again that a tradeoff may exist between the estimates of population numbers and fishing mortality. The model does not fit as well for August and October, presumably because of a shift in gear selectivity or a change in the sampling mechanism. As with the other data sets, selectivity is assumed to be constant throughout the time period of the sample, with estimates $\hat{\alpha}_s = 4.51$ and β_s essentially zero. The growth parameters L_∞ and k are estimated to be 17.53 cm and $0.47 \cdot \text{mo}^{-1}$. A length of 17.5 cm is contained in the 20th length class, indicated in Fig. 5. Figure 6 shows two growth curve trajectories through the relative length–frequencies exhibited by the catch.

Discussion

A length-structured stochastic model is presented as a tool for stock assessment, which differs from existing length-based stock assessment methods (e.g. Jones 1984; Lai and Gallucci

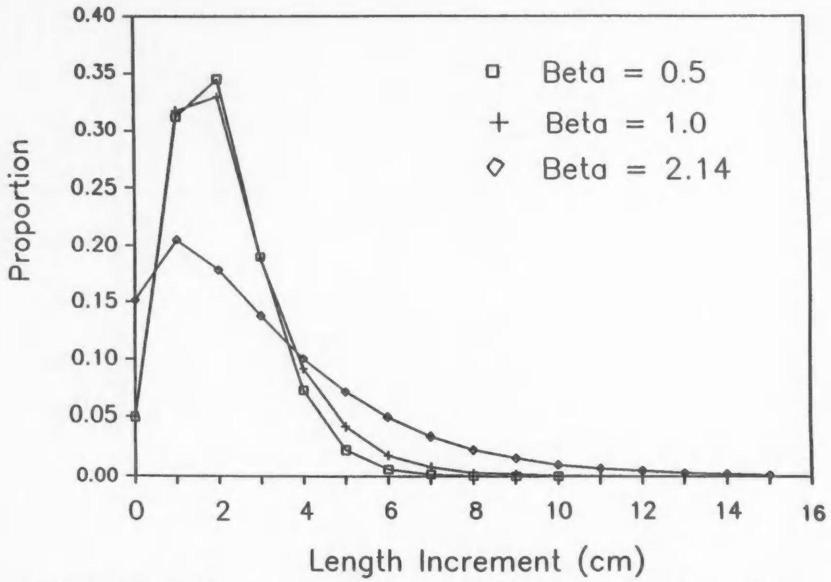

FIG. 2. Distributions of growth increment of fish in the 10-cm length class during a 1-mo period for $\beta = 0.5$, 1.0, and 2.14.

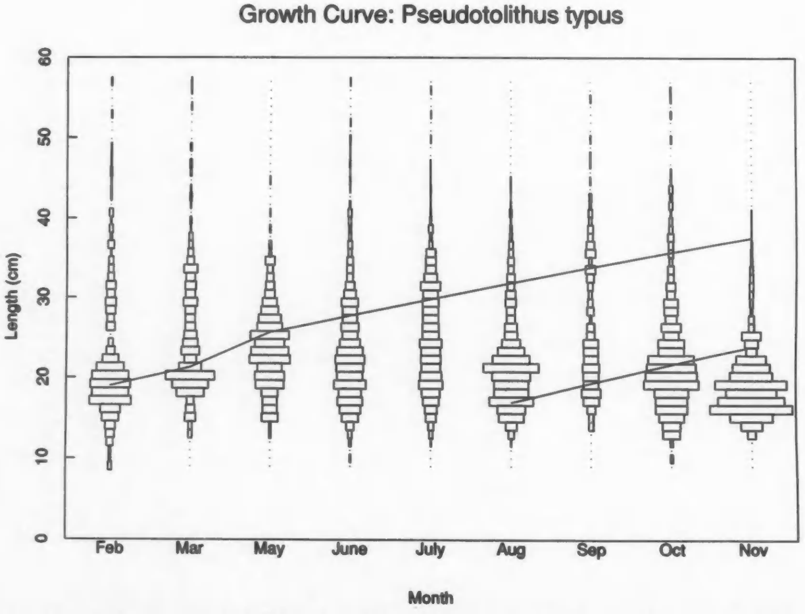

FIG. 3. Growth curve trajectories through catch length–frequencies for *Pseudotolithus typus* based on estimates of $\hat{L}_\infty = 100.17$ cm and $\hat{k} = 0.287\cdot\text{mo}^{-1}$. Each bar indicates the relative catch-at-length.

1988) in many ways. One difference is that growth is included in the model dynamics through a length-based transition matrix whose elements represent growth as the proportion of individuals moving from one length class to another. In this manner, we do not require the assumption of deterministic growth of fish (i.e. growth is identical for all individuals in the population such that all fish of the same age have the same length). The elements of the transition matrix are parameterized in terms of the von Bertalanffy growth parameters, although other paramaterizations with alternative growth models are possible.

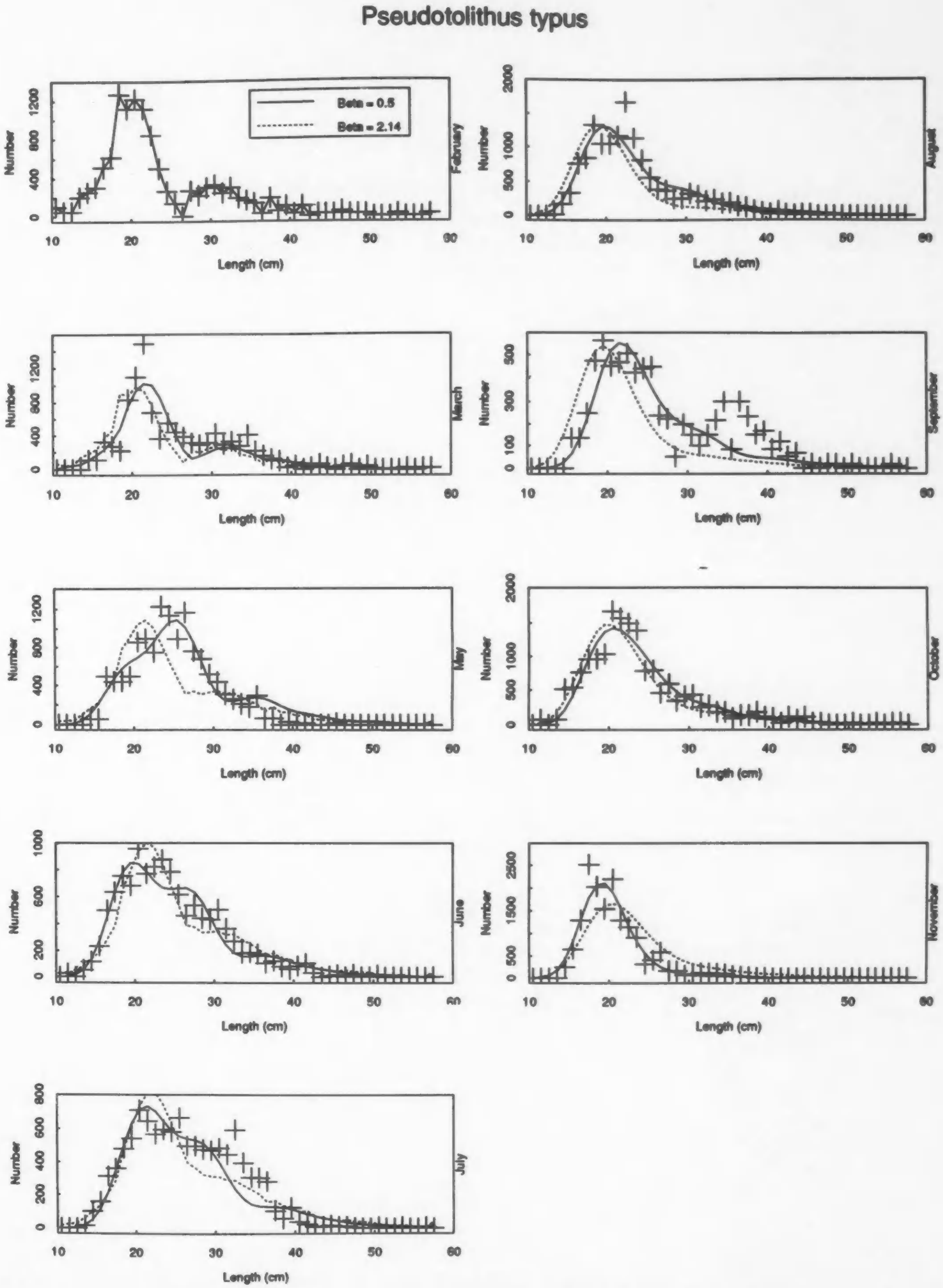

FIG. 4. Observed (+) and estimated (solid and broken lines) catch-at-length of *Pseudotolithus typus* in units of 100 fish for each length class over nine time periods ($\beta = 0.5$, $\beta = 2.14$).

TABLE 4. Parameter estimates of *Decapterus russellii* for three different fixed values of the growth parameter β.

Parameter	Estimate 1 ($\beta = 0.25$)	Estimate 2 ($\beta = 0.35$)	Estimate 3 ($\beta = 0.45$)
N_0	3.4×10^{9}	5.4×10^{9}	6.3×10^{9}
α_r	3.49	8.44	12.26
β_r	1.09	0.52	0.38
R_1	0	0	0
R_2	1.9×10^{10}	3.7×10^{10}	5.0×10^{10}
R_3	0	0	0
R_4	0	0	0
R_5	0	0	0
R_6	0	0	0
R_7	0	0	0
α_s	3.83	4.51	4.81
β_s	0	0	0
f_0	0.0949	0.1575	0.2047
f_1	0.0800	0.0069	0.0063
f_2	0.1114	0.0084	0.0076
f_3	0.0019	0.0011	0.0008
f_4	0.0027	0.0015	0.0011
f_5	0.0016	0.0009	0.0007
f_6	0.0015	0.0008	0.0007
f_7	0.0011	0.0006	0.0005
L_∞	17.59	17.53	17.10
κ	0.47	0.47	0.513
β	0.25^{a}	0.35^{a}	0.45^{a}
M	0.08^{a}	0.08^{a}	0.08^{a}
RSS	8.2×10^{13}	7.7×10^{13}	7.8×10^{13}

[a] Parameters fixed during the estimation procedure.

Another major difference is that we do not require the assumption of steady state. In this manner, we are able to estimate recruitment, abundance, and fishing mortality across time and reflect the dynamics of exploitation over time.

A nonlinear least squares algorithm is used to estimate initial population abundance, recruitment, fishing mortality, selectivity, and the growth parameters simultaneously. As with traditional age-structured analyses (Fournier and Archibald 1982; Deriso et al. 1985), the uniqueness of the parameters is dependent on the structure of the information in the catch and the presence or absence of auxiliary information (e.g. independent sample surveys for the determination of absolute abundance).

The error structure of the observation process was assumed to be additive and independent and identically distributed. In the case of a length-based analysis, and specifically for the examples presented here, additive *iid* error was preferable to multiplicative *iid* error, since the log-transformations that are used for analysis of the latter error tend to obscure the salient features in the dynamics, particularly those representing growth. A more accurate approach perhaps would be to use a length-class specific weighting factor with the weights proportional to the variance associated with each class. Estimating these weights simultaneously with the other parameters is possible, but the estimates computed in this way are often unstable. More sophisticated approaches toward modeling both process and observation error are currently being explored (Mendelssohn 1988; Sullivan 1988).

Because no age information on the population is necessary, this approach can be applied to populations for which ageing is impractical (e.g. no validated ageing methods, substantial ageing errors, etc.). Another possible application is to a fishery targeted on individuals younger than 1 yr old as exemplified by the application to *D. russellii*. However, caution must be exercised in that some estimates of population parameters may not be representative of all life history stages of the species.

The number of parameters to be estimated may seem large but the number is comparable with that estimated by many catch-at-age procedures and is comparable with applications of optimization techniques in the physical sciences. The correlation between various parameter estimates can be made explicit and a sensitivity analysis of the estimates to different assumptions can be made. An examination of the residuals, that is, the difference between observed and expected catch values, along with the associated sum of squares statistic, is one way of determining the appropriateness of the estimates. Other assumptions, such as the approximation of growth by a gamma distribution growth model, can be tested by comparing the estimation results with those obtained under alternative growth models or by comparison with laboratory to field experiments. The sensitivity of the estimates of fixed parameters, which are assumed known, can also be explored.

In all three of the examples discussed above, some parameters were fixed prior to the application of the estimation procedure. In principle, any parameter may be fixed if its value is known. In some instances, it may be necessary to fix a parameter that is not precisely known. The natural mortality parameter M is one such parameter. The estimates of fishing mortality f_t are confounded with M, so M must be fixed to obtain a unique set of estimates. Thus, the best estimates of the f_t's result when M is the best possible; it is important to have a good estimate of M to obtain a good estimate of the f_t's. This issue exists in many stock assessment models, no matter if age or length based (Sims 1984; Lai and Gallucci 1988).

Another set of parameters that may have to be fixed prior to application of the algorithm is that governing the recruitment distribution (i.e. α_r and β_r). It is sometimes necessary to constrain the parameters to a series of likely length categories to prevent confounding of the recruitment distribution with the overall population distribution. Since in some situations recruitment occurs at every time step, it can happen that the recruit population and the adult population become virtually indistinguishable. One way that this may occur is in the steady-state case, where recruitment comes in to replace in each length class the losses due to growth and death. In this case, the length–frequency distribution of the population is the same year after year. Based on length–frequency data alone, it is impossible to distinguish this case from the one where a population exists with no growth, uniform mortality, and no recruitment, or the case where the adult population dies off at the end of the year only to be fully replaced by the new recruits at the beginning of the next year. Constraints are needed to define the estimation surface (e.g. see Hay et al. 1988). In the two examples presented in this paper, it is not necessary to fix these parameters. This is because the samples were obtained at a reasonable temporal resolution and there were periods over which recruitment clearly took place and others where it clearly did not. The recruits entered the fishery as a subpopulation that gradually grew into the main population. Because it was clear when recruitment took place, the recruitment distribution was clearly defined over the appropriate time periods, allowing the estimation surface to be fitted. In other situations, auxiliary information may be available such as independent estimates of recruitment, levels of maturity, or growth, which then can be used to better define the estimation surface.

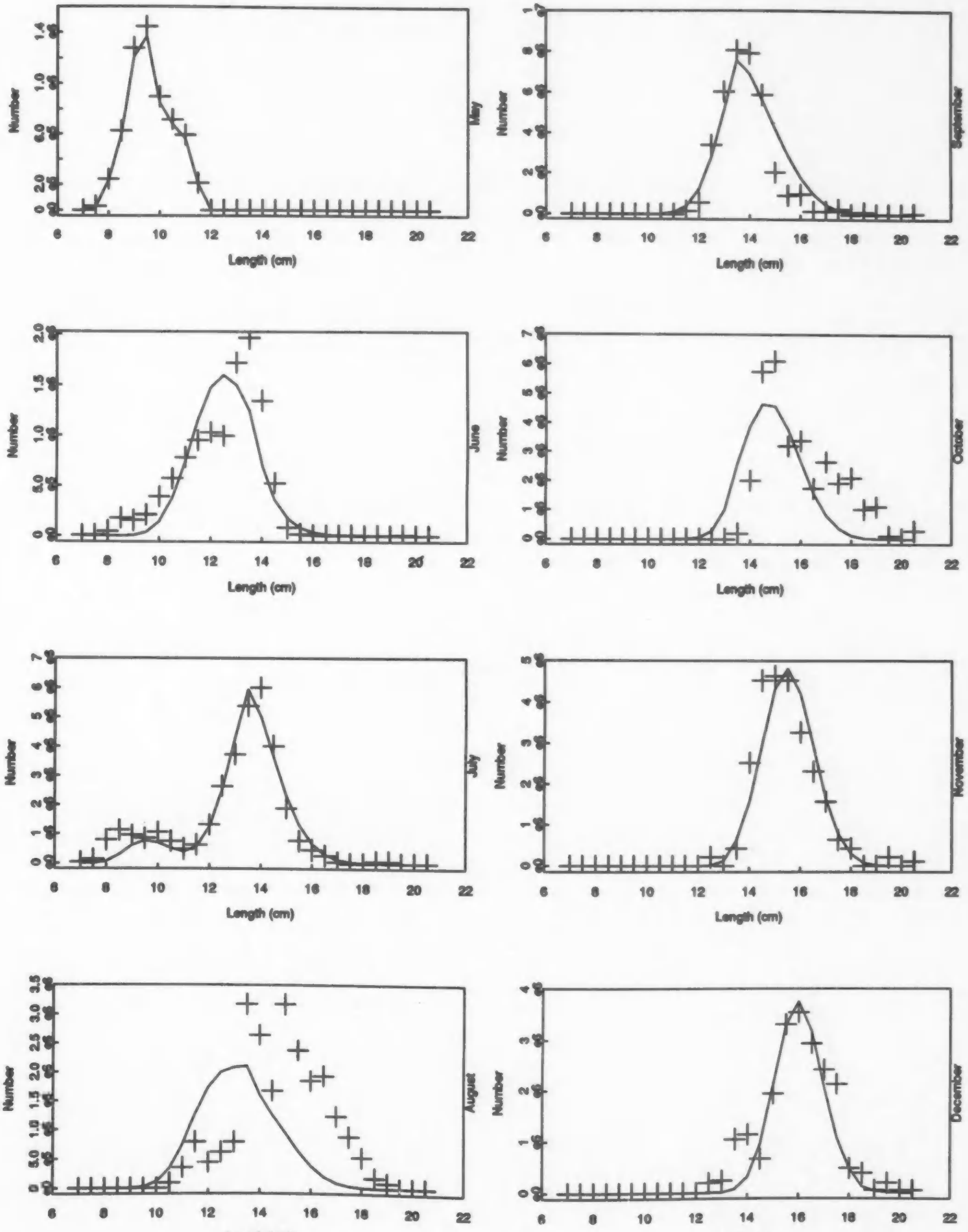

FIG. 5. Observed (+) and estimated (solid line) catch-at-length of *Decapterus russellii* over eight consecutive time periods ($\beta = 0.35$).

Another parameter that sometimes requires greater attention is the growth distribution parameter β. The estimation of this parameter did not always prove feasible under the nonlinear optimization algorithm that we used. In these situations, a reasonable choice for β can be made by systematically fixing β at different values, running the estimation procedure, and choosing a value for β which minimizes the sum of squares obtained over the set of β's. While this approach may not be the best

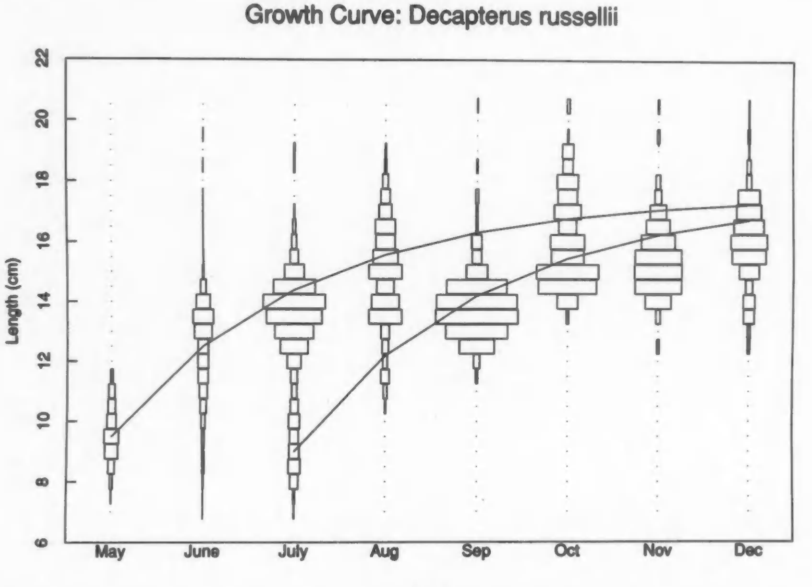

FIG. 6. Growth curve trajectories through catch length–frequencies for *Decapterus russellii* based on estimates of $\hat{L}_\infty = 17.53$ cm and $\hat{k} = 0.47 \cdot \text{mo}^{-1}$. Each bar indicates the relative catch-at-length.

method for estimating β, it worked reasonably well for the case of *D. russellii*. Furthermore, changes in β resulted in relatively minor changes in the other parameter estimates (see Table 4) indicating that the other parameter estimates were fairly robust to the chosen value of β. In the case of *P. typus*, the sum of squares was fairly constant throughout the range of β. In this case, the presence or absence of pattern in the catch residuals was used to indicate which fit was better. Other information, which was not incorporated directly into the model, such as the relative magnitude of recruitment in different months and independent estimates of the growth parameters, was also used to judge the quality of the estimate.

As discussed above in the Model Application and Analysis section, estimates of certain parameters, specifically the growth parameters L_∞ and k for the two commercial fisheries examples, can differ from those obtained by other procedures. In the example of *P. typus*, the growth parameter L_∞ ranges from as low as 61.1 cm to as high as 105 cm, while the corresponding estimates of k range from 0.346 to $0.217 \cdot \text{yr}^{-1}$ (Djama 1988). The catch-at-length analysis presented here estimates $L_\infty = 100.17$ cm and $k = 0.344 \cdot \text{yr}^{-1}$. These estimates are on the extreme end of their ranges, but they do appear to accurately reflect the nature of the stock dynamics as discussed earlier.

In the example of *D. russellii*, Widodo (1988) estimated L_∞ in the range of 24.7 – 28.3 cm and k in the range of 0.39 – $0.50 \cdot \text{yr}^{-1}$ whereas the catch-at-length analysis determined L_∞ to be 17.5 cm and k to be $0.47 \cdot \text{mo}^{-1}$ or $5.6 \cdot \text{yr}^{-1}$. These differences reflect the seasonal growth pattern of incoming 0-yr-old recruits and is consistent with that observed in the year 1 growth of this and related species (Sreenivasan 1982; Widodo 1988). However, it cannot be used to extrapolate the growth of older age fish.

In both examples discussed above, the estimated L_∞ and k adequately describe the growth of individuals represented in the catch. The values of L_∞ and k may differ from those obtained by other means, but together they do provide a good description of the observed growth, and as a consequence, the other simultaneously obtained estimates of abundance, recruitment, and survivorship are reliable relative to this description of growth. One method for examining the range of growth parameter values that provide a similar fit to the set of observations is to examine the two-dimensional projection of the log-likelihood contour surface (Sullivan 1988). For the examples discussed here, this is equivalent to examining the residual sum of squares surface under the optimal parameter estimates while varying the values of two parameters of interest. This can be done for any pairwise comparisons between parameters and, in particular, for the set of growth parameters L_∞ and k.

Given the good fit of the estimates to the simulation data, which represented several years of growth, a series of observations covering several years, taken at monthly or quarterly increments, should provide growth parameter estimates that better reflect the growth of older fish for this species. However, one should avoid tacking the time series onto itself repeatedly to extend the time series sequence for analysis, as the assumption of a recurrent state that this step implicitly makes can severely bias the estimates obtained by any length-based procedure when the assumption is incorrect. If a time series over several years is available, and seasonal variations in growth are expected, then it is interesting to note that the catch-in-length analysis presented here can incorporate the seasonal von Bertalanffy growth model developed by Pauly and Gaschutz (1979), with the power factor $D = 1$, in the form

$$\bar{\Delta}_t = (L_\infty - l)(1 - e^{-k\Delta_s})$$

where

and where Δs is the time since the last period (i.e. $t - t_s$) and n represents the number of time increments in a year (e.g. $n = 12$ for monthly increments of length $\Delta t = 1$). It could also incorporate other growth models such as the Gompertz and Richardson models.

It should also be noted that in the catch-at-length analysis presented here, fishing selectivity and growth are estimated simultaneously; thus, length–frequency maxima that occur in the population, but are not fully reflected in the catch due to selectivity, are accounted for.

In summary, the catch-at-length procedure outlined above provides a general estimation structure through which estimates may be obtained on population size, survivorship, recruitment, and growth. The procedure can be easily modified to account for alternative forms of growth and alternative representations of stochastic variation. However, as with all estimation procedures, care should be given to the quality of the information that is fed into the procedure. The quality of the estimates can only be as good as the quality of the data used by the procedure. For catch data in particular, one fundamental point of concern is that the sample data be representative of the length–frequency distribution observed in the commercial landings. Often, there is not enough information from a single set of samples to provide an adequate picture of what is going on in the population, so data are combined across fishing trips, gear types, management areas, or time periods. Pooling the data must be done only when trends or inconsistencies in the data do not exist. A thoroughly thought-out sampling design followed by a detailed statistical analysis of the data, prior to the application of the catch-at-length algorithm, are necessary to insure high-quality data and to insure that the data are representative of the population of interest.

The program CASA (Catch-At-Size Analysis) used in this analysis is written in FORTRAN 77. The computations presented here were run on a DEC MicroVax II. A user's guide and program on an MS-DOS formatted 5 1/4-inch disc may be obtained from V. F. Gallucci, Management Assistance for Artisanal Fisheries, Center for Quantitative Science, University of Washington, HR-20, Seattle, WA 98195.

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Appendix 1

Instead of estimating all $N_{l,0}$ for $l = 1, \ldots, n$, these variables can be reparameterized into one variable,

$$N_0 = \sum_l N_{l,0},$$

by the following relationshps. Using equation (6) to obtain

$$\text{(A.1)} \quad N_{l,0} = \frac{C_{l,0}(Z_{l,0}}{F_{l,0}(1-e^{-Z_{l,0}})},$$

let P_l be the proportion at length class l in the population. From (A.1):

$$\text{(A.2)} \quad P_t = \frac{N_{l,0}}{N_0} = \frac{C_{l,0}Z_{l,0}/F_{l,0}(1-e^{-Z_{l,0}})}{\sum C_{l,0}Z_{l,0}/F_{l,0}(1-e^{-Z_{l,0}})}.$$

By dividing the numerator and denominator on the right-hand side by $\Sigma C_{l,0} = C_0$, P_l is rewritten as

$$\text{(A.3)} \quad P_l = \frac{q_{l,0}Z_{l,0}/F_{l,0}(1-e^{-Z_{l,0}})}{\sum q_{l,0}Z_{l,0}/F_{l,0}(1-e^{-Z_{l,0}})}$$

where

$$q_{l,0} = \frac{C_{l,0}}{\sum_l C_{l,0}} = \frac{C_{l,0}}{C_0}$$

is the length composition of the catch at $t = 0$. An estimate of the length composition $\hat{q}_{l,0}$ follows from the use of the length distribution of the catch data at $t = 0$, which can be used in equation (A.3) to estimate $\hat{P}_l$.

The length distribution of abundance $N_{l,0}$ can now be estimated from

$$\hat{N}_{l,0} = \hat{P}_l N_0$$

if an initial estimate of N_0 is known. This procedure reduces n estimates of $N_{l,0}$ to one estimate of N_0.

Diel Feeding Chronology and Diet Selection of Rainbow Trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho

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Angradi, T. R., and J. S. Griffith. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. Can. J. Fish. Aquat. Sci. 47: 199–209.

Concurrent rainbow trout (*Oncorhynchus mykiss*) stomach contents and invertebrate drift samples were collected during three 24-h periods in summer 1987. Feeding was discontinuous through the day on all dates. Mean stomach content weight was minimal after 0400 MST and sharply increased between 1000 and 1200 MST on all three dates. Feeding apparently did not occur after twilight. Mean stomach content weight was correlated with water temperature on two dates and was never correlated with invertebrate drift density for non-age-0 trout. Daily ration (wet weight) was 7% of live weight for non-age-0 trout and 21% for age-0 trout. Trichoptera, Ephemeroptera, and Diptera were most important in the diet; terrestrial insects and aquatic vertebrates were rare. The degree of selectivity varied through 24 h and the interpretation depended on the method of analysis used. Occurrence of low-drift cased Trichoptera larvae in stomachs was correlated with amount of filamentous algae ingested, indicating a degree of epibenthic foraging, although no diel pattern could be reliably discerned. Mean length of prey items in stomachs was larger that the drift in 83% of the samples. Our findings support experimentally derived decision rules-of-thumb for foraging trout: select larger prey items, select vulnerable prey, and relax selectivity when hungry.

Des truites arc-en-ciel, *Oncorhynchus mykiss*, des contenus stomacaux et des invertébrés à la dérive ont été échantillonnés durant trois périodes de 24 h à l'été 1987. Au cours de chacune de ces périodes, les poissons se nourrissaient de façon discontinue. Le poids moyen des contenus stomacaux était le plus bas après 4:00 HNR et augmentait rapidement entre 10:00 et 12:00 HNR durant ces trois journées. Il ne semble pas que les poissons se soient nourris après le crépuscule. Le poids moyen des contenus stomacaux était corrélé avec la température de l'eau pour deux des trois périodes et nous n'avons obtenu aucune corrélation entre ce poids moyen et la densité des invertébrés à la dérive pour les truites d'un an et plus. La ration quotidienne (poids frais) des poissons représentait 7 % de leur poids vif dans le cas des poissons de un an et plus et 21 % dans le cas des jeunes de l'année. Leur régime était constitué surtout de trichoptères, d'éphéméroptères et de diptères; les insectes terrestres et les vertébrés aquatiques étaient rares dans les contenus stomacaux. Le degré de sélectivité variait au cours des périodes de 24 h et l'interprétation de ces résultats dépendait de la méthode d'analyse utilisée. La présence de larves de trichoptères, dérivant faiblement, dans les contenus stomacaux était corrélée avec la quantité d'algues filamenteuses ingérées, ce qui montre que les poissons allaient parfois chercher leur nourriture dans la zone épibenthique, mais nous n'avons pu établir si ce comportement suivait une séquence particulière au cours de la journée. La longueur moyenne des proies trouvées dans les estomacs était supérieure à celle des invertébrés à la dérive dans 83 % des échantillons. Nos résultats viennent appuyer les observations expérimentales montrant que les truites en recherche de nourriture s'ajustent aux conditions trophiques : elles sélectionnent les proies les plus grosses et les proies vulnérables, et se montrent moins sélectives quand elles ont faim.

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Many workers have examined foraging behaviour of trout in streams, but a fundamental aspect of their behavioral repertoire, the diel chronology of feeding, has received little attention. Information on the quantity and composition of a fish's stomach contents through 24 h can provide insights that can be incorporated into hypotheses regarding foraging models, microhabitat use, predator avoidance, and the community ecology of stream fishes. Field studies can also be used to test predictions of these hypotheses.

Our review of the stream-dwelling rainbow trout (*Oncorhynchus mykiss*) foraging literature revealed several related axes of debate: nocturnal versus diurnal foraging, drift density dependent versus drift density independent foraging, drift versus epibenthic foraging, and selective versus nonselective foraging.

Jenkins (1969), Tanaka (1970), Jenkins et al. (1970), and Bisson (1978) reported nocturnal feeding by rainbow trout, although their data were equivocal in some cases. Edmundson et al. (1967), Tippets and Moyle (1978), and Johnson and Johnson (1981) reported that feeding by rainbow trout in streams was mostly diurnal. Further, most studies reported a poor correlation between drift density and trout feeding rate as inferred from stomach contents (e.g. Allan 1981; Tippets and Moyle 1978; Bisson 1978) or direct observations (e.g. Griffith 1974; Walsh et al. 1988). Elliott (1970) and Metz (1974), on the other hand, reported positive correlations between drift abundance and feeding. With the exception of Tippets and Moyle (1978), studies of rainbow trout foraging have concluded that food is obtained primarily from the drift. But many studies have reported some degree of epibenthic foraging. Selectivity in foraging based on prey size (Allan 1978; Newman and Waters 1984, and papers cited therein) or prey activity (Ware 1973; Irvine and Northcote 1983; Skinner 1985b) has been demonstrated, but diel variation in the degree of selectivity in feeding has not been examined.

Recent experimentally derived trout foraging models (e.g. Ringler 1979; Bannon and Ringler 1986; Bres 1986) are an improvement over blanket statements made about relative selectivity based on temporally limited diet samples. However, only a few published field studies (e.g. Irvine and Northcote 1982; Dunbrack and Dill 1983; Newman and Waters 1984) have attempted to relate their findings to such models either qualitatively or quantitatively.

In this study, in addition to describing the diet and computing daily rations for two size classes of rainbow trout, we attempted to resolve the apparent controversy over diel foraging by making simultaneous collections of rainbow trout stomach contents and invertebrate drift. We examined diel variation in the amount of food in the stomachs and in the agreement between the composition of the diet and the drift, and we discuss the applicability of foraging models.

Study Area

The Henry's Fork of the Snake River is a fourth-order stream below the confluence with the Buffalo River. In the study reach, mean width of the channel ranges from 60 to 130 m and mean annual discharge is 18 $m^3 \cdot s^{-1}$ (USGS 1989) which is regulated at Island Park Dam. Study site 1 is located 17 km downstream from Island Park Dam; study site 2 is located at Harriman State Park, 4 km upstream from site 1. River discharge in the study reach was 16 $m^3 \cdot s^{-1}$ on 4 June 1987, 39 $m^3 \cdot s^{-1}$ on 17 July 1987, and 22 $m^3 \cdot s^{-1}$ on 12 September 1987. The doubling of flows in late June caused us to use the shallower Harriman Park site. Both study sites were located in broad (75–115 m) riffle-run complexes of low gradient (<0.3%) with surface water velocities of 0.3 – 1.0 $m \cdot s^{-1}$, water depths of 0.2 – 1 m, and gravel substrates. Surface area of the sites was approximately 1.0 ha, which was sufficiently large to allow the sites to be electrofished eight or nine times in 24 h without reshocking specific areas. Riparian cover at both sites was limited to overhanging grass. Instream cover included cobbles, abundant aquatic macrophytes, primarily *Myriophyllum* sp. and *Ranunculus aquatilis*, and surface turbulence.

Water samples collected 0.6 km upstream of site 1 on 24 February 1987 had 3.7 mg total suspended solids$\cdot L^{-1}$, 17 μg total nitrogen$\cdot L^{-1}$ and 30 μg total phosphorus$\cdot L^{-1}$; specific conductance was 166 $\mu S \cdot cm^{-1}$ and pH was 8.09 (Ecosystems Research Institute, Logan, UT, unpubl. data). Water temperature ranged from 10 (September) to 20°C (June). Mean diel variation in water temperature was 6°C. Summer water temperatures in the study areas rarely exceed 23°C or fall below 9°C (Whitehead 1978; Angradi and Contor 1988). There was a partial moon on all sampling dates. It was overcast and there were rain showers on 17 July; the weather was clear on the other sample dates.

Methods

Twenty-four-hour studies were conducted between 0300 and 0430 Mountain Standard Time (MST) at site 1 on 4 June 1987 and at site 2 on 17 July and 12 September 1987. Rainbow trout were collected at 3-h intervals by electrofishing from an aluminum drift boat equipped with a 5000-W generator, Coffelt variable voltage pulsator (Coffelt Electronics Company, Englewood, CO), and a single fixed boom or throwable anode. Eight fish samples were collected on 4 June and 12 September; nine fish samples were collected on 17 July. Captured rainbow trout were anaesthetized (tricainemethanesulfonate), weighed to the nearest gram, and length was measured to the nearest millimetre.

TABLE 1. Sample sizes, mean lengths (mm) and weights (g), estimated mean relative stomach content weights (RWW), gastric evacuation coefficients (*R*), C_{24} (daily ration) expressed as (i) RWW, (ii) RDW, and (iii) dry weight of stomach contents as a percent of dry fish weight, and percentage of empty stomachs for rainbow trout collected in summer 1987 from the Henry's Fork River, Idaho. *R* values were estimated from the observed decrease in stomach contents after the feeding peak. Values for age-0 rainbow trout are given in parentheses.

	4 June	17 July	12 September
Total *N*	69	91 (64)	121
Mean *N*	9	10 (7)	15
SD mean *N*	2	3 (3)	3
Mean length	177	220 (73)	202
SD length	15.9	22.7 (6.4)	25.4
Mean weight	70.5	139.4 (4.4)	108.1
SD weight	17.9	46.0 (1.1)	37.8
Mean RWW	1.9	2.1 (5.9)	1.8
SD RWW	1.8	4.3 (1.7)	2.1
R	0.2	0.1 (0.2)	0.2
C_{24i}	7.1	6.6 (21.4)	7.0
C_{24ii}	0.5	0.4 (1.4)	0.5
C_{24iii}	2.0	1.8 (5.6)	1.9
% empty	7.2	2.2 (3.1)	13.0

Mean number of fish captured varied between intervals and dates. Number and size of fish captured are given in Table 1. In all cases, we attempted to capture as many fish as possible within 1 h following the beginning of the sample interval. One-way analysis of variance (ANOVA) indicated that there was no effect of time of day on the mean length of fish captured on any date. On 17 July, age-0 trout were present in the sample and had a mean length of 73 mm. Data from age-0 trout were analysed separately from older trout unless otherwise specified. Age-0 trout captured on 12 September were not distinguishable from age-1+ trout on the basis of length, and probably had similar diets (see Miller 1974). Data in Angradi and Contor (1988) indicate that most non-age-0 rainbow trout included in this study were age 1+ and 2+.

Stomach contents were removed by pulsed gastric irrigation using a modification of Foster's (1977) technique. Trout <100 mm were held over a collecting jar and pumped twice with pulsed flow with 5 mL of water via a blunted 18-gauge hypodermic needle. Trout 100–250 mm were pumped twice with 15 mL of water via a blunted 14-gauge cannula. Trout >250 mm were pumped twice with 30 mL of water through a 5-mm-diameter plastic tube fitted to a collecting funnel. Pumped fish were revived, fin-clipped (to avoid resampling), and released. Stomach contents were preserved in the field in ethanol (70%). In the laboratory, stomach contents were drained, blotted to remove superficial water, and weighed to the nearest milligram on a tared analytical balance. Stomach content weights were divided by live body weight and multiplied by 100 to yield a relative stomach content wet weight (RWW) for each fish. Fish with a RWW <0.1% were considered to have empty stomachs.

After weighing, stomach samples were sorted to the lowest practical taxonomic level (usually genus), enumerated, and invertebrates were separated into 2-mm size categories (cerci excluded). Only whole invertebrates and inhabited Trichoptera cases were counted. All stomach samples were subjectively scored according to the amount of ingested plant material: stomachs without plant material were scored 0, and stomachs in which plant material was present were scored 1–3 depending on the amount of material. Finally, stomach samples were oven dried at 50°C to a constant weight and weighed to the nearest 0.1 mg. To allow comparison of our results with studies reporting only dry weights, relative dry weight (RDW) in milligrams dry weight of stomach contents per 100 mg live fish weight was regressed on RWW for all fish, and the following equation was obtained:

$$(1)\quad \mathrm{RDW} = 0.018 + 0.063\ \mathrm{RWW} \qquad (r^2 = 0.76,\ P < 0.0001).$$

We assumed that the dry weight of trout was 24% of the live weight (Elliott 1975).

Invertebrate drift was collected coincident with electrofishing. Five drift nets with 136.5-cm^2 openings and 0.243-mm mesh were positioned across the channel upstream of the area of the electrofishing activity. On 17 July, emerging mayflies (primarily *Baetis*) were abundant, so drift nets were positioned to include surface drift. On 4 June and 12 September, nets were positioned at 0.6·total depth. Drift was collected for 20 min; sample flow volume was calculated from velocity measurements made with a Swoffer model 2100 velocity meter at the net mouth. Invertebrate samples were processed the same as the stomach samples except they were not dried or weighed. Water temperature was measured at each sample interval.

For each sample date, ANOVA was used to test the hypothesis that feeding by rainbow trout, as determined by the RWW of stomach contents, was discontinuous through the diel period (Jenkins and Green 1977). For the 17 July sample, separate ANOVA analyses were conducted for age-0 and non-age-0 trout. In the models tested, RWW was the dependent variable, and time of day was the independent classification factor. Examination of residuals indicated a nonconstant error variance, so we made the transformation $\mathrm{RWW}' = (\mathrm{RWW} + 1)^{0.5}$ (Neter et al. 1985). Tukey's (HSD) studentized range test (Neter et al. 1985) was used to make multiple comparisons among sample interval means for each date.

Mean daily rations (C_{24}) were calculated for each sample date using Eggers' (1977) model:

$$(2)\quad C_{24} = 24\,SR$$

where S is the mean RWW over 24 h and R is the gastric evacuation rate as an exponential decay function (Brett and Higgs 1970; Elliott 1972). R was estimated from the observed decrease in mean RWW during the night (Walsh et al. 1988) on 17 July and 12 September. The semi-log transformation of the exponential regression model (Elliot 1972) was used:

$$(3)\quad \ln y = \ln a - Rx$$

where y is the percentage reduction in mean RWW, a is the intercept, and x is the time since the feeding peak.

The Spearman rank correlation coefficient (r_s, Siegel 1956) was used to test for associations among mean RWW, mean drift density, and water temperature and to compare the relative proportion of each of 16 prey categories in the pooled drift sample with the relative proportion in the pooled trout stomach sample for each sample interval (sensu Elliott 1970; Allan 1981).

The index of overlap (C_H) between the diet and the drift was computed using the Horn (1966) modification of the simplified Morisita index (Krebs 1989):

$$(4)\quad C_H = 2 \sum_{i=1}^{s} ripi \Big/ \left(\sum_{i=1}^{s} ri^2 + \sum_{i=1}^{s} pi^2 \right)$$

where C_H is the overlap coefficient, s is the number of food categories, ri is the proportion of total stomach content sample contributed by food category i, and pi is the proportion of total drift sample contributed by food category i. C_H varies between 0 (no categories in common) and 1 (identical proportional composition), with overlap coefficients >0.60 indicating significant overlap (Zaret and Rand 1971). All 42 prey categories were included in the analysis.

A chi-square test of independence was used to test for diel variation in mean drift density and diel variation in the percentage of trout stomachs in each sample containing plant material. One-way ANOVA was used to test the hypotheses that mean length of invertebrates in the drift and in the stomachs was constant through the diel period.

Results

Feeding was discontinuous through the diel period for all sample dates and age classes ($P < 0.01$) (Fig. 1). Multiple comparisons among sample intervals within dates indicate that a significant increase in RWW occurred after 1200 on 17 July and 12 September (Fig. 1b and 1c). Peak mean within-sample RWW was 3.4% on all dates for non-age-0 trout and was 8.3% for age-0 trout on 17 July. RWW generally declined through the night (Fig. 1b and 1c) and was at a minimum near dawn (Fig. 1a and 1c), indicating that after twilight, rainbow trout fed little or not at all. The observed chronologies for the three dates are similar despite differences in biotic (e.g. total drift density, size of fish) and abiotic conditions (e.g. weather, water temperature).

Mean daily RWW ranged from 1.8 to 2.1% for the three dates (excluding age-0 trout) (Table 1), and means were not significantly different from each other (Mann–Whitney U-test, $P > 0.05$). Peak individual RWW ranged from 8.8 to 10.2%. For age-0 trout, mean and peak individual RWW were 5.9 and 20.4%, respectively. Mean RWW for age-0 trout was significantly higher (Mann–Whitney U-test, $P < 0.05$) than for non-age-0 trout. Daily ration (C_{24}) was similar on all dates (Table 1) for non-age-0 trout (approximately 7% of live weight) and was much higher, 21.4%, for age-0 trout on 17 July.

The percentage of empty stomachs in the sample ranged from 2.2 to 13% (Table 1), indicating that most fish were feeding. The coefficient of variation of RWW was inversely correlated ($r_s = -0.51$, $P < 0.05$) with mean RWW (pooled for all dates, $n = 25$), suggesting that when mean feeding activity was low (as inferred from stomach contents), some fish had empty stomachs, and some fish were either feeding or still had food in their stomachs from a previous meal. When mean feeding activity was higher, variability was lower, and few fish had empty stomachs.

For non-age-0 trout, the density of drifting invertebrates was not correlated with mean RWW on any date. There was a slight positive correlation between mean RWW and drift density for age-0 trout ($r_s = 0.67$, $P < 0.1$); in this case, age-0 trout were

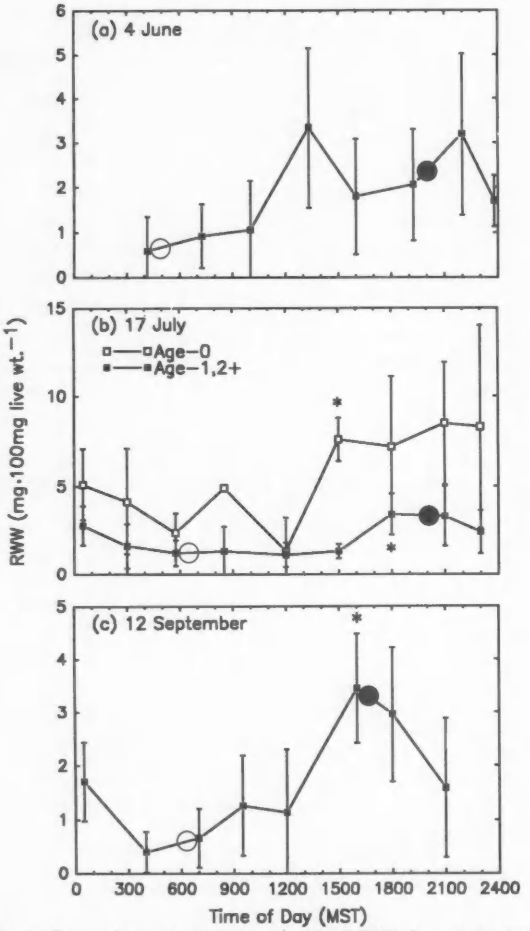

FIG. 1. Change in mean relative wet weight (RWW) through the diel period of stomach contents of rainbow trout collected on three dates in summer 1987 on the Henry's Fork River, Idaho. Error bars denote 95% confidence intervals. Asterisks denote values significantly different from the previous value (Tukey's HSD, $P < 0.05$). On 17 July, no confidence interval was calculated for mean RWW of age-0 fish at 0300 due to a very small sample size ($N = 2$). Sunrise is indicated by an open circle and sunset by a solid circle. Sample sizes for each diel sample are given in Table 1.

apparently exploiting a heavy diurnal *Baetis* emergence (Table 2b; Fig. 1b and 2). Diel variation in drift density was nearly significant ($P = 0.13$) on 4 June and highly significant on 17 July and 12 September. Drift density exhibited the expected pattern (Fig. 2) of low densities during the day with a sharp increase after sunset (Waters 1962; Kroger 1974; Allan 1987). If drift density accounted for the observed diel pattern in RWW, drift and RWW would vary together, with peak RWW shifted to the right of peak drift due to a lag in gastric evacuation (Allan 1981). On all dates the afternoon or dusk increase in RWW preceded the increase in drift density (Fig. 1 and 2).

On 12 September, RWW was positively correlated with water temperature ($r_s = 0.9$, $P < 0.01$); there was a slight positive correlation ($r_s = 0.68$, $P < 0.1$) between RWW and water temperature on 4 June. Drift density was not significantly correlated ($P > 0.10$) with water temperature on any date.

The relative proportions by number of specific taxa in the stomach contents varied between sample intervals, but three orders, Trichoptera, Ephemeroptera, and Diptera, numerically dominated the stomach content samples (Table 2). On 4 June, Ephemeroptera nymphs (primarily *Ephemerella* and *Baetis* spp.) were most important and comprised from 18 to 69% (mean = 37%) of the stomach contents. Adult Trichoptera were also important, ranging from 1 to 58% (mean = 26%) of the stomach contents. On 17 July, adult Ephemeroptera, including emerging subimagos, were the most important category, comprising from 3 to 82% (mean = 66%) of age-0 and from 2 to 91% (mean = 54%) of non-age-0 stomach contents. Larvae of *Brachycentrus* spp. ranged in percentage composition from 2 to 67% (mean = 27%) of non-age-0 stomach contents but were not important in age-0 stomachs (mean = 0.4%). On 12 September, the relative contribution of food categories was more even. Adult Ephemeroptera were most important, comprising from 6 to 78% (mean = 36%) of the stomach samples. *Baetis* nymphs comprised between 0 and 42% (mean = 14%) of the stomach samples. Taxa that were generally rare in the stomach samples were abundant in some samples: terrestrial insects and aquatic Coleoptera larvae were important in several samples on 4 June, and adult and larval aquatic Diptera were occasionally important on 17 July and 12 September. Plecoptera were not abundant in any sample. Of 345 rainbow trout stomachs examined, 2 (0.6%) contained vertebrate prey items (fish). The mean number of prey items per stomach was 37 (SD = 23.9) on 4 June 1987, 64 (SD = 54.9) for age-0 trout and 161 (SD = 146.3) for non-age-0 trout on 17 July 1987, and 93 (SD = 84.8) on 12 September 1987. The mean number of prey items per stomach was highly rank correlated with mean RWW on all dates. Since large, highly calorific items were rare in the diet and the drift, our analysis of stomach samples based on the relative proportion by number was probably a robust one.

The relative percentage composition of the drift samples was generally concentrated into fewer categories than the stomach contents (Table 2). On 4 June, Ephemeroptera nymphs were the most numerous drifting taxa and ranged in percentage composition from 14 to 74 (mean = 35%). Adult Trichoptera comprised 21% of the drift sample. On 17 July, adult Ephemeroptera and *Baetis* nymphs dominated, comprising 30 and 20% of the drift sample, respectively. On 12 September, *Baetis* dominated six of eight samples (mean = 70%) and comprised over 98% of three samples. Terrestrial invertebrates were rare in the drift in the July and September samples; Trichoptera larvae and snails were rare in the drift on all dates. Plant material was rare in the drift and was excluded from the analysis. The mean number of prey items per drift sample was 14 (SD = 13.4) on 4 June, 83 (SD = 67.1) on 17 July, and 186 (SD = 251.0) on 12 September.

Forty-seven (SD = 18.0) and 30% (SD = 16.0) of the stomachs on 17 July and 12 September, respectively, contained vegetation, almost exclusively filamentous algae (Table 2). Plant material dominated the sample by volume (vegetation score of 3) of 11.5% (SD = 11.9) and 10.2% (SD = 12.6) of the stomachs on the respective dates. No stomachs of fish collected on 4 June 1987 contained vegetation. On 17 July, only 3% of the stomachs (two fish) of age-0 trout contained aquatic vegetation.

On both dates, the percentage of stomachs in the sample that contained vegetation varied significantly through the diel period, although no pattern could be discerned. The percentage

TABLE 2. Percentage composition of the stomach contents of rainbow trout (*r*) and drift samples (*p*), water temperature, and percentage of stomachs containing aquatic vegetation during the diel period on three dates in summer 1987 on the Henry's Fork River, Idaho: (a) 4 June, (b) 17 July, and (c) 12 September. On 4 June, no stomachs contained aquatic vegetation. For 17 July, values for age-0 rainbow trout follow values for non-age-0 trout, i.e. non-age-0/age-0. Total number is the total number of invertebrates in the pooled stomach and pooled drift samples. Categories within Trichoptera, Ephemeroptera, and Plecoptera are for immatures unless otherwise indicated. Sample sizes are given in Table 1.

(a) Time of day (MST), 4 June 1987

Taxon	0410		0715		1000		1320		1600		1915		2200		2400	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Trichoptera																
Adults	1.0	6.5	4.8	9.5	30.3	33.3	10.3	4.8	16.4	16.2	58.0	41.9	56.0	38.6	35.2	14.1
Hydropsyche sp.	19.6	2.6	8.8	4.8	7.2	7.4	9.5	2.4	7.1		3.5		1.2		4.7	2.0
Brachycentrus sp.	4.9	0.6	3.2	9.5	1.0	3.7	5.0	4.9	5.3		1.3		2.0		1.5	
Glossosoma sp.	2.9														0.4	
Amiocentrus sp.	1.0								0.2				0.3		3.9	
Unknown larvae			0.8				0.4								0.4	
Ephemeroptera																
Adults	11.8	4.5	0.8		10.1	11.1	15.7	17.0	16.8	5.4	1.0	2.3	6.6		0.4	
Drunell sp.	4.9	4.5	3.2		1.9		5.8		0.2				0.4		1.9	0.5
Ephemerella sp.	32.3	12.3	61.6	28.6	24.5	3.7	17.8	4.9	20.7	8.1	19.7	2.3	10.5	2.3	28.9	10.6
Ephemera sp.	5.9				1.4						0.3				1.6	
Baetis sp.	6.9	52.3	3.2	4.8	3.4	22.2	5.4	9.8	3.7	16.2	5.3	11.6	7.6	18.2	9.4	53.8
Rithrogena sp.		1.9	0.8				0.4		0.2		0.2				0.8	0.5
Siphlonurus sp.		2.6														5.5
Ameletus sp.		0.6													0.8	
Plecoptera																
Adults			0.8				1.7		0.9				0.1			0.5
Hesperoperla sp.	1.0				1.4				0.7		0.5		0.3		0.8	
Isoperla sp.	2.0	1.3	0.8		0.5						0.3				0.8	
Pteronarcys sp.	1.0															
Alloperla sp.		0.6													0.8	0.5
Claassenia sp.			0.8													
Acroneuria sp.							0.4									
Unknown nymph											0.3				0.8	
Diptera																
Adults	2.0	0.6		14.3	3.4	3.7	13.6	7.3	8.1	16.2	0.3	2.3	5.1	15.9	1.6	1.0
Pupae			4.0		7.2	3.7	5.3		13.1		2.3		7.5		4.7	1.0
Larvae		0.6	4.0	4.8	1.9	3.7	2.5	2.4	1.2		1.3		0.7		0.4	
Miscellaneous Aquatic invertebrates																
Coleoptera		7.1		19.0			0.4	14.6					0.1			4.5
Hemiptera																1.0
Lepidoptera					0.5				0.2		0.3					
Odonata	1.0															
Amphipoda			0.8				0.4		0.5		0.8	2.3				1.5
Oligochaeta					2.9		0.4									
Hirudinea	1.0															
Terrestrial insects			1.6	4.7	2.4	7.4	5.0	31.7	4.6	37.8	4.8	37.2	1.3	22.7	0.4	3.0
Fish		1.3														
Total number	102	155	25	21	208	27	242	41	434	37	395	43	761	44	256	199
Water temperature (°C)	12.5		13.0		15.0		15.0		20.0		20.0		18.0		15.0	

of stomachs with vegetation was weakly correlated with the proportion of Trichoptera larvae in the sample on 17 July (Pearson's $r = 0.49$, $P = 0.18$) and 12 September (Pearson's $r = 0.58$, $P = 0.14$). The correlation was improved for 17 July (Pearson's $r = 0.59$, $P = 0.09$) when the mean proportion of Trichoptera larvae in each trout stomach was used, probably because in pooling trout stomachs in diel samples, the influence on the sample of individual trout feeding heavily on Trichoptera larvae was reduced.

Agreement between percentage taxonomic composition of the stomach contents and the drift varied dramatically through the 24-h period on all dates and depended on the method of calculation. On 4 June, six of eight stomach content samples were positively rank correlated with the drift, and four of eight stomach content samples overlapped significantly ($C_H > 0.60$) with the drift (Table 3). On 17 July, seven of eight stomach content samples were rank correlated with the drift for age-0 and non-age-0 trout; four (non-age-0) and three (age-0) of eight samples significantly overlapped. On 12 September, four of eight stomach samples were rank correlated with the drift and two significantly overlapped.

Degree of overlap varied through the day. For example, on 17 July, C_H for age-0 trout ranged from 0.02 to 0.99. On 12 September 1987, C_H ranged from less than 0.001 to 0.76 in subsequent diel samples (i.e. from 0400 to 0700 MST. In all cases, C_H was lowest after 2400 MST and increased after about 0400 MST. Mean agreement between stomach contents and the drift varied among dates for both r_s and C_H. Mean C_H was significantly lower (Mann–Whitney *U*-test, $P < 0.05$) on 12 September than on other dates. Mean r_s on 12 September was significantly lower (Mann–Whitney *U*-test, $P < 0.1$) than on 17 July.

On 17 July, the percentage composition of age-0 and non-age-0 trout stomach contents was significantly correlated for seven of nine diel samples, and eight significantly overlapped (Table 4). Degree of overlap was highest in evening and at night, when the stomach samples of both age groups were dominated by adult Ephemeroptera.

TABLE 2. (*Continued*)

	(b) Time of day (MST), 17 July 1987																
	0030		0300		0545		0830		1200		1500		1800		2100		2300
Taxon	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*
Trichoptera																	
Adults	3.2/7.6	9.3	3.6/3.0	7.7	9.8/2.5	10.2	0.3/2.8	9.8	2.1/3.3	1.9	0.7/2.1	0.1	0.6/3.2		1.4/3.9	0.9	2.0/2.8
Hydropsyche sp.	0.1	0.2	0.4			2.2			1.7		0.2				0.1		0.4/0.1
Brachycentrus sp.	2.5	0.9	3.8/0.1	0.2	12.3		67.0	4.9	20.6	5.6	23.1	0.1	5.6/1.2	1.3	14.4/0.3	1.5	9.5/1.7
Glossosoma sp.	0.3/0.9	0.2	0.4		1.0		0.3		1.7		1.1/0.2		0.2/0.2		1.8/0.9		0.4/0.2
Amiocentrus sp.	0.2		0.3				0.3		0.3								
Limnephilus sp.			0.1														
Mysticides sp.	0.1						1.3		0.7		0.2		0.1/0.2		0.1/0.1		
Unknown larvae					1.2						0.1						
Ephemeroptera																	
Adults	77.8/77.8	5.1	84.0/71.3	0.8	26.3/64.3	18.6	2.3/69.7	7.3	8.0/3.3	9.3	54.4/79.4	99.1	90.9/80.2	94.0	70.6/74.5	85.6	68.5/81.9
Drunella sp.									1.7								
Ephemerella sp.	1.2/1.2	12.0	1.0/4.1	2.3	5.4/6.3		2.3/5.5	2.4	1.4/16.7	3.7	0.8/2.9	0.2	1.4	1.0	0.3/3.4	1.1	1.2/0.3
Ephemera sp.				0.2	1.3	1.7					0.2						
Baetis sp.	2.7/2.7	53.7	0.9/7.8	87.7	29.5/11.8	45.8	9.6/1.8	26.8	4.5/20.0	22.2	5.6/1.0	0.1	0.1/3.6		1.9/4.6	0.2	9.1/6.7
Rithrogena sp.					0.4										0.1		
Siphlonurus sp.		1.3	0.1/0.7	0.2			0.3										1.0
Ameletus sp.		0.2	0.3	0.3	0.3												
Callibaetis sp.					0.6												0.1
Tricorythodes sp.			0.7				0.3				0.1/1.5		0.9		0.1	0.2	
Plecoptera																	
Adults									0.3								
Hesperoperla sp.									0.3								
Isoperla sp.		0.2		0.2													
Unknown nymph	0.1										0.1						
Diptera																	
Adult	6.7/7.3	16.4	2.5/8.9	0.3	1.3/6.3	20.3	1.0/6.4	46.3	24.5/40.0	57.4	8.4/7.1	0.3	1.7/5.2	0.8	4.6/8.1	10.2	4.8/5.4
Pupae	0.7/3.0		1.7/1.1		0.3/3.4		2.6/7.3		4.9/6.7		2.3/1.5		0.1/1.9		1.0/2.6	0.2	0.4/0.5
Larvae	2.6/1.6		0.2/0.7		1.9/4.6		8.6/1.0		5.9/6.7		0.9/2.5		1.6		1.3/0.9	0.2	1.1/0.1
Miscellaneous aquatic invertebrates																	
Coleoptera	0.1				0.6		4.6		0.3		0.6						
Amphipoda	0.1		0.1	0.3	1.6/0.4		3.0		0.7		1.6				0.5		0.4
Oligochaeta									17.5				0.1		0.5		0.2
Gastropoda	0.3/0.2		0.3						1.4		0.2		0.1		0.1		0.1
Nematoda	0.1/0.2								0.7/3.3						0.1/0.1		0.1/0.1
Terrestrial insects	1.1/0.7	0.2	0.5/0.4	0.2	3.5	3.4	0.7/1.0	2.4	0.3		0.4		0.3/0.4	3.0	1.0/0.4		1.1/0.3
Fish	0.1		0.1														
Total number	1331/437	432	867/268	665	316/238	59	303/109	41	286/30	54	857/477	928	6304/561	398	2809/701	47	2524/1391
Aquatic vegetation	57.1/0	—	42.6/12.5	—	44.5/0	—	80.0/0	—	30.0/0	—	25.0/10	—	30.8/0	—	63.6/0	—	53.9/0
Water temperature (°C)	13		13		13		13		15		15		16		15		14

Mean length of invertebrates in the stomach was larger than that of the drift on all dates (Wilcoxon signed rank test; 4 June, 12 September: $P < 0.05$; 17 July: $P < 0.1$) (Table 5). ANOVA indicated that mean length of invertebrates did not vary significantly through the day. The effect of time of day was significant ($P < 0.01$) for stomach contents on 4 June and for the drift on 17 July. In both cases, however, only one sample was different from any of the others (Tukey's HSD test, $P < 0.05$) (Table 5). To test the hypothesis that larger taxa (and larger individuals within taxa) drift and are consumed by trout at night (Allan 1978, 1984; Bisson 1978), we pooled prey item lengths for all stomach and drift samples collected during the day (0600–2000 MST) and at night. ANOVA indicated that time of day (day or night) had a significant effect on the mean length of drifting invertebrates on 17 July and a near significant ($P = 0.13$) effect on 12 September. Time of day had a slightly significant effect on the mean length of invertebrates in the stomachs only on 12 September. In all cases for the stomach and drift, significant or not, mean length was greater at night, supporting Allan's (1978, 1984) drift/predation risk hypothesis.

Discussion

Eggers (1977) proposed a simple model to describe the diel trajectory of food in the stomach of fish:

$$(5)\quad dS/dt = F - RS$$

where S is the instantaneous amount of food in the stomach, t is time, F is the rate of food intake (Elliott 1975), and R is the gastric evacuation rate (see equation (3)). Our data for RWW levels through the diel period (Fig. 1) resemble Eggers' Case I and II feeding regimes (Eggers 1977, fig. 2). In Case I, F is constant during the daylight period and is at or near zero after dusk; the shape of the diel trajectory is convex upward. In Case II, F increases continuously during the daylight period and is zero at other times; the shape of the diel trajectory is concave upward. The actual case for the rainbow trout we sampled is likely intermediate. The correlation we noted between water temperature and mean RWW implies that F may have increased during the period of feeding, particularly on 17 July and 12 September. Within the range of preferred temperature, a slight increase in water temperature can substantially hasten gastric evacuation (Brett and Higgs 1970), stimulating an increased feeding rate via autonomic feedback (Grove et al. 1978). Our interpretation appears to corroborate Elliott (1975) who demonstrated a positive relationship between temperature and F for brown trout over a similar temperature range.

Jenkins (1969) and Tanaka (1970) found that rainbow trout were able to feed on drifting invertebrates at night in experi-

TABLE 2. (*Concluded*)

	(c) Time of day (MST), 12 September 1987															
	0400		0700		0930		1200		1600		1800		2100		0030	
Taxon	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Trichoptera																
Adults			3.6	1.0	10.5	1.9	4.3	11.1	0.8	2.2	1.0		1.1		2.1	
Hydropsyche sp.	2.3				1.0	1.9	0.1		0.3		0.2	1.8	0.3		0.4	
Brachycentrus sp.	47.7		6.8		8.2		2.5		0.5	2.2	0.4		3.1	0.1	3.0	
Glossosom sp.	4.5		0.1		7.1		1.8		0.3		0.3		1.6		0.2	
Limnephilus sp.															0.2	
Mystacides sp.					0.3		0.1		0.1	2.2	0.6	1.8	1.6		0.1	
Helicopsyche sp.	13.6		1.6	1.3			0.1	5.6		19.6	0.1		1.5		0.4	
Unknown larvae			0.4										0.1		0.3	
Ephemeroptera																
Adults	11.4	0.1	12.0		6.1		43.0		78.1	4.3	69.2	3.6	22.7	0.2	45.5	0.1
Ephemerella sp.	6.8		0.4	2.6		7.5		5.6		2.2	0.2	3.6	0.2	0.1	0.1	
Baetis sp.		99.2	42.4	81.5	32.0	58.5	17.1	27.8	3.3	45.7	7.7	53.5	8.2	98.4	4.5	98.7
Rithrogena sp.	9.1	0.1														
Ameletus sp.				7.0	0.3											
Plecoptera																
Unknown nymph					0.3									0.1		
Diptera																
Adults	2.3	0.1	22.4	1.3	4.8		15.5	27.8	5.3		4.1	3.6	9.9	0.1	8.6	0.1
Pupae		0.1	1.6	2.0	3.4	1.9	5.9		2.1	6.5	4.7	8.9	3.4	0.2	1.9	0.1
Larvae	2.3	0.3	3.6	7.9	22.8	17.0	6.4	5.6	4.8	4.3	4.3	8.9	43.3	0.3	29.0	0.4
Miscellaneous aquatic invertebrates																
Coleoptera		0.1	0.4	1.0	0.3	3.8	0.1	16.7				3.5			0.1	0.4
Amphipoda			0.8		0.7		1.3		1.5	4.3	2.0	1.8	2.1	0.1		
Oligochaeta					0.3				0.1		0.4	1.8				
Hirudinea						1.9								0.1		
Gastropoda		0.1	0.8	0.7	0.7		1.2		0.1		0.1		0.2		0.2	0.1
Nematoda					0.3											
Cladocera									0.3		1.5		0.3		1.4	
Terrestrial insects		0.1	2.4		0.7	5.7	0.2		2.2	6.5	3.3	7.1	0.3	0.1	1.6	
Total number	44	1565	250	151	294	53	1357	18	4878	46	3035	56	941	2808	1165	2760
Aquatic vegetation	50.0	—	8.3	—	50.0	—	18.8	—	21.1	—	29.4	—	46.2	—	23.1	—
Water temperature (°C)	11.5		10.0		12.0		14.0		17.0		16.5		15.0		12.5	

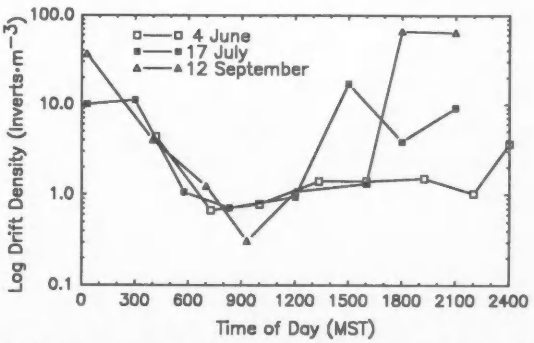

FIG. 2. Change in mean drift density (number of invertebrates per cubic metre of flow through a drift net) through the diel period on three dates in summer 1987 on the Henry's Fork River, Idaho.

mental stream channels. Jenkins et al. (1970) felt that rainbow trout in a Sierra Nevada stream were "willing and able to feed [on drifting invertebrates] 24 hr a day." However, their data (Jenkins et al. 1970, fig. 1) more closely resemble Eggers' (1977) Case II feeding regime in which feeding did not occur at night. Data presented by Bisson (1978, table 1) for hatchery rainbow trout closely resemble our data for 17 July (Fig. 1) except that in his study, peak feeding occurred much earlier in the day, before 1200. Data presented by Johnson and Johnson (1981, fig. 1) for age-0 steelhead in New York also agree with our findings. Elliott (1973) reported that rainbow trout in a French stream exhibited a feeding peak after dusk, but probably did not feed after midnight. Robinson and Tash (1979) found that Apache trout in the laboratory were unable to feed on drift at light intensities less than moonlight. These studies and the data presented herein (see also Hoar 1953; Stringer and Hoar 1955; Edmundson et al. 1967; Tippets and Moyle 1978) provide compelling evidence that wild rainbow trout generally do not feed at night in summer.

Comparisons of C_{24} estimates among disparate studies are complicated by uncertainties concerning sizes of fish used, evacuation rate estimates, methods (e.g. in situ versus experimental), and the units of expression (Windell et al. 1976; Amundsen and Klemetsen 1988). With these caveats, our estimates are within the range reported elsewhere for salmonids and obtained under similar conditions (i.e. similar water temperatures, fish size). For example, our estimate of 5.6% for age-0 rainbow trout (Table 2; C_{24iii}) exceeds that of Doble and Eggers (1978) for juvenile sockeye salmon (approximately 2.5%) but is less than the values reported by Brodeur and Pearcy (1987) (10–15%) for juvenile coho salmon and by Walsh et al. (1988) (7–10%) for age-0 brook trout. Estimates reported by Elliott (1975, table 8) for similar-sized brown trout are two to three times larger than ours, but his estimates are based on a higher estimate of *R*. Our estimates of C_{24} may be underestimates because we calculated *R* based on nighttime water temperatures and the assumption of no feeding after the feeding peak.

TABLE 3. Spearman rank correlation coefficients (r_s) and overlap coefficients (C_H) calculated from the percentage composition by number of the stomach contents of rainbow trout collected from the Henry's Fork River in summer 1987 and the percentage composition of the invertebrate drift. For 17 July, values for age-0 trout are given in parentheses. For each r_s, $N = 17$; for each C_H, $N = 42$. C_H values equal to or greater than 0.6 are significant. Significant r_s values: $*P < 0.05$; $**P < 0.1$. Prey categories used in the calculation of r_s include Trichoptera adults, *Hydropsyche* sp., *Brachycentrus* sp., other Trichoptera larvae, Ephemeroptera adults, *Ephemerella* sp., *Baetis* sp., other Ephemeroptera larvae, Plecoptera adults, Plecoptera larvae, Diptera adults, Diptera pupae, Diptera larvae, Coleoptera, other aquatic invertebrates and fish, and terrestrial insects.

4 June			17 July			12 September		
Time	r_s	C_H	Time	r_s	C_H	Time	r_s	C_H
0410	0.55*	0.38	0300	0.60*(0.62)*	0.12 (0.02)	0400	−0.22	0.00
0715	0.26	0.68	0545	0.52*(0.57)*	0.51 (0.82)	0700	0.35	0.76
1000	0.71*	0.76	0830	0.32 (0.51)*	0.22 (0.17)	0930	0.17	0.81
1320	0.51*	0.55	1200	0.53*(0.60)*	0.90 (0.49)	1200	0.33	0.44
1600	0.55*	0.48	1500	0.64*(0.61)*	0.97 (0.47)	1600	0.56*	0.13
1915	0.55*	0.76	1800	0.58*(0.40)	0.98 (0.99)	1800	0.77*	0.20
2200	0.65*	0.81	2100	0.67*(0.76)*	0.99 (0.97)	2100	0.49**	0.13
2400	0.41	0.48	0030	0.57*(0.62)*	0.19 (0.15)	0030	0.60*	0.07
Mean	0.52	0.61		0.55 (0.59)	0.51 (0.61)		0.38	0.32
SD	0.14	0.16		0.11 (0.10)	0.38 (0.39)		0.31	0.32

TABLE 4. Spearman rank correlation coefficients (r_s) and overlap coefficients (C_H) calculated for the percentage composition by number of the stomach contents of age-0 and non-age-0 rainbow trout collected 17 July 1987 from the Henrys Fork River, Idaho. For each r_s, $N = 17$; for each C_H, $N = 42$. C_H values equal to or greater than 0.6 are significant. Significant r_s values: $*P < 0.05$.

Time	r_s	C_H
0300	0.66*	0.98
0545	0.39	0.68
0830	0.19	0.05
1200	0.54*	0.62
1500	0.58*	0.88
1800	0.56*	0.99
2100	0.78*	0.98
2300	0.83*	0.98
0030	0.77*	0.99
Mean	0.56	0.79
SD	0.23	0.31

The rainbow trout population we studied apparently did not exploit the nocturnal increase in drift density. Our study corroborates other studies that indicate that feeding activity in stream-dwelling salmonids is not well correlated with drift density (Bisson 1978; Allan 1981), and trout do not exploit the nighttime increase in drift density (Tippets and Moyle 1978; Griffith 1974; Walsh et al. 1988). Elliott, however, found a good correlation between diel changes in drift density and the amount of food eaten by rainbow trout in a French (Elliott 1973) and an English stream (Elliott 1970; cf. Chaston 1969).

The summer diet of wild rainbow trout in streams has been described in a scattered literature. All the recent studies we reviewed reported that four aquatic taxa, Ephemeroptera, Trichoptera, Plecoptera, and Diptera, dominated the diet (Tebo and Hassler 1963; Jenkins et al. 1970; Antonelli et al. 1972; Elliott 1973; Metz 1974; Wagner 1975; Tippets and Moyle 1978; Johnson and Ringler 1980; Johnson and Johnson 1981; Irvine and Northcote 1982; Johnson 1985; Richards and Soltz 1986; Cada et al. 1987). These taxa, except for Plecoptera, also dominated the stomach contents we examined, which is not surprising, since approximately 90% (by number) of the benthos of most Rocky Mountain streams is composed of these four taxa (Andrews and Minshall 1979, table 3). All of the studies we reviewed were conducted in streams much smaller (particularly in channel width) than the Henry's Fork, and, contrary to our findings, they generally show that terrestrial insects are consistently well represented in the diet of rainbow trout.

The importance of substrate-oriented foraging by stream-dwelling trout is not well known (Ringler and Brodowski 1983; Newman 1987), and it is apparently quite variable (Allen 1969; Waters 1969). Bisson (1978) reported that rainbow trout occasionally consumed Trichoptera larvae in large numbers; he felt most were taken from the substrate at night. We also found highest relative proportions of Trichoptera larvae in the stomach at dawn on 4 June and 12 September, but Trichoptera larvae are evacuated slowly and may accumulate in the stomach (Elliot 1972, Windell and Bowen 1978). Tippets and Moyle (1978) found a positive association between low-drift taxa and the amount of algae in the stomachs of trout. We agree with their interpretation that this material is ingested accidentally during epibenthic foraging. McAfee (1966) stated that algae were more frequently found in rainbow trout stomachs than in other trout species.

Perhaps the strongest conclusion from our analysis of the agreement between the composition of the drift and the diet is that the relationship varies through the diel period and between dates. Inferences based on samples collected on a single date or at restricted times of day may be misleading. Rank correlation, a technique used in two often-cited papers (i.e. Elliott 1970; Allan 1981), suggested a closer agreement between the drift and the diet than did the overlap index (Table 4), although both methods revealed diel variation in diet–drift agreement. Assuming that close agreement (strong rank correlation, high overlap) results from nonselective foraging and poor agreement results from selective foraging, the use of rank correlation alone is likely to bias the interpretation in favor of nonselective foraging in which trout are simply feeding randomly from the food categories present in the drift. When many food categories are used, the large number of ties for rare taxa produces an inflated estimate of agreement. When categories are collapsed, selection within higher level taxa will be masked. The overlap index

TABLE 5. Mean length (mm) of invertebrates in the stomachs of rainbow trout and invertebrate drift samples collected from the Henry's Fork River in summer 1987. Mean lengths for 17 July are for the pooled sample of age-0 and non-age-0 trout. No drift sample was collected at 2300 MST on 17 July. Mean values that are significantly larger (Tukey's HSD test, $P < 0.05$) than at least one other value on that date for the same category (stomach or drift) are indicated by an asterisk.

4 June			17 July			12 September		
Time	Stomach	Drift	Time	Stomach	Drift	Time	Stomach	Drift
0410	7.98*	4.99	0300	4.41	4.18	0400	4.92	3.86
0715	6.22	4.96	0545	4.15	4.10	0700	4.22	3.66
1000	6.94	4.68	0830	4.92	3.80	0930	4.06	3.63
1320	6.63	5.48	1200	4.22	3.85	1200	4.02	3.84
1600	5.77	4.96	1500	4.58	4.00	1600	3.87	3.88
1915	5.23	4.91	1800	4.14	4.27	1800	3.62	3.74
2200	5.14	4.77	2100	4.46	4.10	2100	3.89	3.98
2400	5.63	4.78	2300	4.58	—	0030	4.45	3.82
			0030	4.06	4.48*			
Mean	6.19	4.94		4.39	4.10		4.13	3.80
SD	0.96	0.24		0.28	0.22		0.40	0.12

(C_H) is not influenced by ties or seriously biased by rare taxa. This approach, unlike rank correlation, tends to overemphasize abundant taxa, but since the estimate is based on a pooled sample of individual fish that probably vary considerably in what they are exposed to in the drift and what they eat (Bryan and Larkin 1972; Ringler 1983), it is probably a conservative measure of agreement. We calculated the proportional similarity index (PS) (Feinsinger et al. 1981) for all diel samples. The PS has been proposed as an appropriate measure of an organism's dietary specialization (Feinsinger et al. 1981). In all cases the PS was highly correlated with C_H (4 June: $r_s = 0.90$, $P<0.005$; 17 July (both age groups), 12 September: $r_s = 0.98$, $P<0.001$). Therefore, the use of PS leads to identical conclusions as the use of C_H did.

For decades most studies found trout in streams to be nonselective, consuming foods in proportion to their availability (Needham 1930; Nyman 1970, and papers cited therein; Ware 1972; Cada et al. 1987). Several recent studies have identified selective feeding by trout (e.g. Allen 1941; Metz 1974; Allan 1978; Ringler 1979). Bisson (1978) concluded that trout fed selectively from the drift in an experimental stream. Overlap values calculated from his data (Bisson 1978, table 2) support his conclusions: for both large and small trout, only one of seven diel samples significantly overlapped. His drift samples were dominanted by minute terrestrial Collembola (P. A. Bisson, pers. comm.) which may have been outside the acceptable prey size range (sensu Griffiths 1975), nonpalatable, or completely novel to his trout. When we reanalysed his data with Collembola omitted, four of seven diel samples significantly overlapped for both sizes of trout, suggesting that diel variation in degree of selectivity in foraging may be a general phenomenon.

Our study was not intended as a test of foraging models, but our findings are interesting in this regard. Bres (1986) demonstrated that rainbow trout diet selection was strongly influenced by the relative abundance of prey types rather than the calorific content of prey items. He felt that trout were using nonoptimal rules-of-thumb in making feeding decisions. Such rules do not require that the forager have a perfect knowledge of prey energy values or encounter rates (Townsend and Winfield 1987), and should prove valuable in understanding trout foraging in situ where spatial and diel variability in the prey item assemblage is high. Such rules may include: select more visible prey items, select items larger than the minimum prey size threshold (Krebs 1978; Bannon and Ringler 1986; Bres 1986), select prey that are easy to catch and handle (Townsend and Winfield 1987), and relax selectivity when hungry (Murdoch et al. 1975; Dill 1983).

Our findings support these experimentally derived rule-of-thumb hypotheses. Trout were size selective; the mean length of items in the stomach (all taxa pooled) was larger than in the drift in 83% of the diel samples (Table 5). That trout are size selective has been well demonstrated (Allan 1978; Newman and Waters 1984; Skinner 1985a), but if size selection alone was accounting for the observed diet of trout, the agreement between the percentage composition of the diet and the drift (by taxa) would not be as close as we found. We conclude that in order to fill their stomachs, trout are usually constrained to consume small, suboptimal-sized prey items (sensu Bannon and Ringler 1986) in the relative proportions in which they occur, even in food-rich streams like the Henry's Fork. Indeed, Bres (1986) has demonstrated experimentally that under the constraints of stomach capacity and gastric evacuation rate, a stomach full of suboptimal-sized small items represents more energy than a stomach containing a few large items, even if the large items are individually more energy rich. Within prey categories, trout are likely to select the relatively larger, more visible items by rule-of-thumb, thus accounting for the observed size selection.

Trout showed a strong preference for adult mayflies when they were present in the drift. Adult mayflies floating on or near the surface as imagos or subimagos were ostensibly the most vulnerable and visible types of prey encountered (excluding terrestrial insects which were generally rare) (Dunbrack and Dill 1983; Wilzbach et al. 1986). Many of the cases of nonsignificant overlap on 17 July and 12 September were due to trout feeding disproportionately on adult mayflies.

If trout were least selective when they were hungry, then degree of overlap should increase after the morning minimum as trout resume feeding on empty stomachs. This was the case in our study on all three dates for non-age-0 trout (Table 3); no clear trend is apparent for age-0 fish.

Optimal foraging models such as rules-of-thumb are useful as a general background against which to organize observations about individual behavior. More studies are needed to identify the interrelationships among decision rules-of-thumb and related questions (e.g. Do trout use different rules at different times of day? Do different sized trout use different rules? How does stream productivity influence degree of selectivity in foraging? and to provide the empirical basis for evaluating other salmonid foraging hypotheses.

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Effects of Aluminum on the Leopard Frog, *Rana pipiens:* Life Stage Comparisons and Aluminum Uptake

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Freda, J., and D. G. McDonald. 1990. Effects of aluminum on the leopard frog, *Rana pipiens*: life stage comparisons and aluminum uptake. Can. J. Fish. Aquat. Sci. 47: 210–216.

In this study, we conducted a series of toxicity tests investigating the response of embryos, prestage 25 tadpoles and 3-wk old tadpoles of the leopard frog (*Rana pipiens*) to a wide range pf pH (4.2–4.8) and Al (0–1000 $\mu g\cdot:L^{-1}$), and to pH 6.5 with no Al present. In embryos and prestage 25 tadpoles, Al ameliorated the toxic effects of very low pH's (4.2–4.4), while becoming toxic at higher pH's (4.6–4.8). Although both embryos and prestage 25 tadpoles were killed by low pH (pH 4.2–4.4 and 4.2, respectively) and elevated Al (≥500 and ≥250 $\mu g\cdot L^{-1}$ Al, respectively), embryos were relatively more sensitive (i.e. higher percent mortality) to low pH, whereas prestage 25 tadpoles were relatively more sensitive to Al. Three week old tadpoles did not die at any test pH (without Al) and mortality (>20%) caused by Al occurred at only pH 4.8 and 750–1000 $\mu g\cdot L^{-1}$ Al. The body sodium concentrations of 3-wk old tadpoles that survived high Al exposure were depressed indicating sublethal stress. Whole body Al uptake in 3-wk old tadpoles was also elevated in water containing high concentrations of Al, but it was positively related to water pH and exposure time. This result suggests that body Al content is not an accurate indicator of Al exposure in tadpoles living in acidic, Al contaminated ponds.

On a mené une série de tests de toxicité afin de déterminer la réaction d'embryons, de têtards au pré-stade 25 et de têtards de trois semaines de la grenouille léopard (*Rana pipiens*) soumis à un grand écart de pH (4, 2–4, 8) et de concentrations de Al (0–100 $\mu g\cdot L^{-1}$) ainsi qu'à un pH 6,5 en l'absence de Al. Chez les embryons et les têtards au pré-stade 25, la présence de Al a augmenté l'incidence toxique de très faibles pH (4,2–4,4) pour devenir toxique à des pH plus élevés (4,6–4,8). Même si un faible pH (4,2–4,4 et 4,2, respectivement) et une concentration élevée de Al (500 et 250 $\mu g\cdot L^{-1}$ Al, respectivement) étaient mortels pour les embryons et les têtards au pré-stade 25, les embryons étaient relativement plus sensibles (pourcentage de mortalité plus élevé) à un faible pH tandis que les têtards au pré-stade 25 étaient relativement plus sensibles au Al. Les têtards de trois semaines ne sont pas morts après l'exposition aux pH expérimentaux (en l'absence de Al) et la mort (20 %) résultant de l'exposition à Al n'a eu lieu qu'au ph 4,8 et à des concentrations de Al allant de 750 à 1 000 $\mu g\cdot L^{-1}$. Les concentrations corporelles de sodium chez les têtards de trois semaines qui ont survécu après l'exposition à une concentration élevée de Al étaient abaissées; ceci est un indicateur de stress subléthal. L'absorption de Al chez les têtards de trois semaines était aussi élevée en milieu contenant des concentrations élevées de Al mais elle était en relation positive avec le pH de l'eau et le temps d'exposition. Ce dernier résultat porte à croire que la teneur corporelle de Al n'est pas un indicateur précis de l'exposition au Al chez les têtards qui vivent dans des étangs acides contaminés de Al.

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Mounting evidence has suggested that acidic precipitation is causing the death of amphibians in some regions (see review by Freda 1986). In addition, many species of amphibians can not survive exposure to the naturally acidic waters of sphagnum bogs and blackwater systems (Gosner and Black 1957; Saber and Dunson 1978). Regardless of the source of the acidity (anthropogenic or natural), the pH of breeding ponds has a dramatic impact on the local distribution and abundance of amphibian species. The toxic action of acidic water can cause direct mortality of embryos and larvae or can inhibit the growth of larvae which may indirectly lower survival (Freda and Dunson 1985a and 1986; Cummins 1986).

Predicting the toxicity of pond water to amphibians has proven difficult because as pH declines, the concentrations of many toxic metals increase. The most notable is Al, whose solubility dramatically increases as water pH drops below 5.0. Aluminum, an extremely abundant element in soils, enters aquatic systems through acidified surface or subsurface runoff after rainstorms, or from direct leaching from the pond's sediments. The interpretation of Al toxicity is difficult because of its complex speciation which is controlled by pH and the presence of inorganic and organic ligands. In acidic water, Al may exist as Al^{3+}, AlF, or $AlSO_4$, while aqueous $Al(OH)_x$ complexes predominate at higher pH's. Aluminum can also form soluble complexes with inorganic ligands such as humic acid. For fish, it is generally agreed that Al^{3+} and hydroxide complexes are the most toxic, fluoride complexation reduces toxicity, and organic complexes are nontoxic (Driscoll et al. 1980;

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TABLE 1. The ionic composition of pH 6.5 artificial soft water (ASW) used for rearing of animals and experimentation (N.D. = not detectable; DOC = dissolved organic carbon.)

Ion	(mg L^{-1}) Concentration
Na	2.5
K	0.6
Ca	1.3
Mg	0.7
Mn	(N.D.)
Ni	(N.D.)
Pb	0.004
Fe	0.009
Cu	(N.D.)
Cd	0.008
Zn	(N.D.)
Al	0.002
Cl	4.3
SO_4	0.6
F	0.068
DOC	1.0

Schofield and Trojnar 1980; Neville 1985). In contrast, Clark and LaZerte (1985) found no difference in toxicity between Al^{3+} and AlF to amphibians.

A complete understanding of Al toxicity to amphibians has not yet emerged. Some field studies have clearly demonstrated Al toxicity to amphibians (Clark and Hall 1985; Freda et al. 1990), whereas others have found no correlation between Al and embryonic mortality or amphibian abundance (Dale et al. 1985a; Clark 1986; Gascon and Planas 1986). This is not at all surprising given the complex nature of Al toxicity and interspecific and intraspecific variation in sensitivity to Al (Clark and LaZerte 1987; Freda et al. 1990). Laboratory studies of Al toxicity have also suggested possible influences of water pH and amphibian life stage (Clark and LaZerte 1985; Dale et al. 1985b; Gascon et al. 1987).

Therefore it was the objective of this study to determine the pattern of Al toxicity in the leopard frog (*Rana pipiens*) over a range of pH and at discrete life stages. This particular species has been previously shown to be one of the most sensitive to acidic water (Freda and Dunson 1984). In this study, we have measured Al toxicity of a wide range of concentrations and at four different pH's to three separate amphibian life stages: embryos, prestage 25 tadpoles, and 3-wk old tadpoles. In addition, we measured body sodium concentrations of tadpoles as an indicator of sublethal stress because it is well known that low pH and Al disrupt sodium balance in amphibians (Freda and Dunson 1984; Gascon et al. 1987). We also measured body Al concentration to see if Al uptake is a good indicator of Al exposure.

Materials and Methods

Animals

Adult leopard frogs (*Rana pipiens*) were obtained from Northwest Biological Laboratories. Female frogs were induced to ovulate by injection of frog pituitaries and analytical grade progesterone (Rugh 1962). Since we were interested in describing the general pattern of Al toxicity in *R. pipiens*, we only used eggs and tadpoles from one pair of frogs (i.e. all tests animals were full siblings) in order to reduce variability. If we were attempting to describe the toxicity of Al to *R. pipiens* from a specific region, we would have tested eggs from several different clutches. Eggs were stripped into a culture dish containing frog sperm in 10% amphibian ringers. The eggs were then transferred to artificial soft water (ASW, Table 1) 30 min later. Tadpoles were reared in ASW at room temperature (20 ± 2°C) and ambient lighting, and fed commercial trout food. Tadpoles were fasted 1d prior to and during experiments to reduce pH drift and organic complexation of Al. The average mass (mean + SD) of tadpoles used for experiments was 50 ± 29 mg ($n = 250$).

Water Chemistry

All experiments and the rearing of embryos and tadpoles were done in ASW which was made by the dilution of dechlorinated tap water (1:40) with ion free water from an ion exchange column. The chemical composition of ASW is listed in Table 1. The pH's of experimental solutions were checked twice daily with a Markson model 88 pH meter and Cole Palmer glass electrode, and readjusted to the desired pH with H_2SO_4. The concentration of Al was manipulated by the addition of varying amounts of an $AlCl_3$ stock solution. Although Cl^- also co-varied with Al, the relatively small addition even in the highest Al treatment (3.9 $mg \cdot L^{-1}$) is not sufficient to influence toxicity (Freda and Dunson 1985b). Our test water also contained 68 $\mu g \cdot L^{-1}$ F, similar to the mean concentration of 61 $\mu g \cdot L^{-1}$ for 91 ponds surveyed in central Ontario (Freda et al. 1990). The addition of 100 $\mu g \cdot L^{-1}$ F has also been shown not to affect Al toxicity in two other species of amphibians (Clark and LaZerte 1985). The Al concentration of the water was measured at the start and end of experiments by the catecol-violet method (Dougan and Wilson 1974; Seip et al. 1984). Aluminum was fractionated into total monomeric Al, labile Al (free), and nonlabile Al (bound) by use of ion exchange column methodology (Driscoll 1984). The concentrations of Na^+, K^+, Ca^{2+}, Mg^{2+}, Cu^{2+}, Cd^{2+}, and Zn^{2+} were determined by atomic absorption spectrophotometry (Varian model 1275). All other chemical analyses were performed by the Ontario Ministry of the Environment, Rexdale, Ontario.

In all experiments, pH control was achieved and drift never exceeded 0.08 units. The concentrations of Al measured at the beginning of the experiments were always within 4% of nominal (expected) levels. After 96 h, the concentrations of Al at pH 4.2, 4.4, and 4.6 generally increased by 3–7% due to evaporation. At pH 4.8, the concentrations of Al at 250 and 500 $\mu g \cdot L^{-1}$ increased by 3–5%, while it dropped by 3–5% at 750 and 1000 $\mu g \cdot L^{-1}$. Organic complexation of Al was negligible (<3%) in all experiments. Nominal concentrations of Al are reported, hereafter.

Experimental Matrix and Test Containers

Embryos, prestage 25 tadpoles, and 3-wk old tadpoles were all exposed to an identical matrix of pH (4.2, 4.4, 4.6, 4.8, 6.5) and Al (0, 250, 500, 750, 1000 $\mu g \cdot L^{-1}$). These pH's and Al levels bracket values reported for amphibian breeding ponds (Freda and Dunson 1986; Albers and Prouty 1987; Freda et al. 1990). Only 0 $\mu g \cdot L^{-1}$ Al was used at pH 6.5 because of the low solubility of Al at this pH. Test chambers were constructed from sheets of polyethylene plastic, cut into the shape of a cross, and sealed along opposing sides with heat (commercial freezer bag sealer). This formed a water tight container (15 × 15 × 20 cm) that had excellent resistance to the binding of Al, and could be collapsed for easy storage. Each bag was filled with 1 L of experimental water. While most Al toxicity tests on fish have employed flow-through, nonrecirculating water delivery, our use of static tests is entirely appropriate. Most ephemeral breeding ponds are small and stagnant (no inflows or outflows).

Toxicity Tests

Embryos

Thirty embryos were placed in each test container 3 h after fertilization (2–4 cell stage; stage 3–4, Gosner 1960). Each cell of the experimental matrix was replicated three times. Each day until hatching which took approximately 4–5 d, the number of living and dead embryos was noted, and qualitative descriptions of abnormalities were recorded. Dead embryos did not promote fungus growth and were not removed.

Prestage 25 tadpoles

The eggs not employed in embryo toxicity tests were incubated in pH 6.5 ASW for later use in tadpoles toxicity tests. One to 3 h after hatching, 10 newly hatched tadpoles (stage 20, Gosner 1960) were placed into each cell of the experimental matrix (three replicates). The toxicity test continued until animals reached stage 25 (closure of operculum, Gosner 1960) which was approximately 96 h. Death was defined as the lack of response to mechanical stimuli and dead tadpoles were removed from experimental solutions.

Three-week old tadpoles

Tadpoles not used for the preceding experiment were reared for 3 wk in pH 6.5 ASW and then exposed to the experimental matrix for 96 h ($n=10$ tadpoles per replicate, three replicates tested). Tadpoles were at stage 25 during testing. We checked for dead tadpoles every 30 min for the first 15 h of the experiment and every 1 to 5 h thereafter.

Body Na and Al Content of 3-wk old Tadpoles

All 3-wk old tadpoles from one of the replicates were removed at death or after 96 h, lightly blotted on tissue paper, weighed (0.001 g accuracy) and dissolved in 1mL of 3N HNO_3 at 50°C. Aliquots were removed, diluted in distilled water, and then analyzed for sodium by atomic absorption spectrophotometry. Another aliquot was removed, diluted, and analyzed for Al using a modification of the catecol-violet method (Driscoll 1984). The amount of catecol-violet used was increased by four times and the reaction time was increased from 30 min to 24 h to insure complete reaction with any "tightly" bound Al. We also spiked digests of tadpoles reared in Al-free ASW with known, variable amounts of Al. The absorption curve for this spiked assay was almost identical to the curve for standards used for water analysis indicating no interferences.

Statistical Analysis

All data are reported as means ±1 SE of the mean (SEM). Two way analysis of variance was used to test if either pH and/or Al treatment had a significant effect on percent mortality or body concentrations of sodium or Al. To achieve a balanced design, the pH 6.5, 0 $\mu g \cdot L^{-1}$ Al cell was not included in the analysis. The number of dead animals in the three replicates within a treatment were summed and then divided by the total number of animals in the treatment to arrive at a percent mortality value. Percent mortality data were then transformed using an arc-sine square root transformation before statistical testing (Steel and Torrie 1960). Statistical differences between chosen pH and Al treatments and the control treatment were determined by using two sample *t*-tests ($p<0.05$). The 96 h LC50 and 95% confidence interval for Al at each pH was calculated by the moving average method using measured values for total monomeric Al (Stephan 1977).

Results

Mortality of Embryos

The pH and the concentration of Al in experimental solutions had a significant effect ($p<0.001$) on the survival of embryos (Fig. 1A). Virtually all control embryos hatched (99±1% at pH 6.5 and 0 $\mu g \cdot L^{-1}$ Al), whereas most embryos (94%) failed to hatch at pH 4.2, At pH 4.2 and 4.4, the addition of Al (250–1000 $\mu g \cdot L^{-1}$) ameliorated the effects of low pH and permitted hatching of most embryos (78–99%). At pH 4.6 and 4.8, the situation was completely reversed and Al was extremely toxic. Mortality was significantly increased at 750 and 1000 $\mu g \cdot L^{-1}$ Al at pH 4.6 and at 500 to 1000 $\mu g \cdot L^{-1}$ Al at pH 4.8. The LC50 for Al at pH 4.6 and 4.8 was 811 and 403 $\mu g \cdot L^{-1}$, respectively (95% CI's: 773–847 and 371–448 $\mu g \cdot L^{-1}$).

The mechanism by which embryos were killed also varied depending upon the pH and concentration of Al. For example, at pH 4.2 and 0 $\mu g \cdot L^{-1}$ Al, development was arrested during the first 12 h of exposure for 99% of dead embryos. In the other experimental cells where mortality was greater than 30%, the prominent cause of death (92% of dead embryos) was the inability of embryos to escape from their vitelline membranes at hatching. These embryos assumed a curled appearance due to the tight constriction by the vitelline membrane. However, embryos at pH 4.2 and 250 to 1000 $\mu g \cdot L^{-1}$ Al were also curled, but were able to hatch. We also noticed that in many of the treatments containing Al (see Fig. 1A for asterisks), newly hatched tadpoles developed discrete edematous sacs on the exterior surface of their bodies. Tadpoles with these fluid filled sacs rested on the bottom and had great difficulty swimming, while normal tadpoles clung to the sides of the container and swam vigorously when disturbed. Many (6–18%) of these abnormal tadpoles died within 12 h of hatching.

Mortality of Prestage 25 Tadpoles

Prestage 25 tadpoles required approximately 96 h to complete development to the free swimming stage (stage 25). Control mortality at pH 6.5 and 0 $\mu g \cdot L^{-1}$ Al was 0%. Both pH and Al had significant ($p<0.001$) effects on the survival of prestage 25 tadpoles (Fig. 1B). Prestage 25 tadpoles were less sensitive to low pH than embryos with only 20% mortality occurring at pH 4.2 and 0 $\mu g \cdot L^{-1}$ Al. However, prestage 25 tadpoles were much more sensitive to Al than embryos. All tadpoles died at Al concentrations ≥500 $\mu g \cdot L^{-1}$ at pH 4.4 and 4.6, and at ≥250 $\mu g \cdot L^{-1}$ at pH 4.8. As described in the previous section, Al toxicity was accompanied by characteristic swellings on the surface of animals which in severe cases, spread over the entire body surface and gave the tadpole a "balloon-like" appearance. In addition, although tadpoles in several experimental cells were not technically dead, they were swollen, could not swim, and failed to reach stage 25 (see Fig. 1B for crosses).

Mortality of 3-wk old Tadpoles

Three-week old tadpoles were less sensitive to lowered pH and elevated Al than either embryos or newborn tadpoles (Fig.

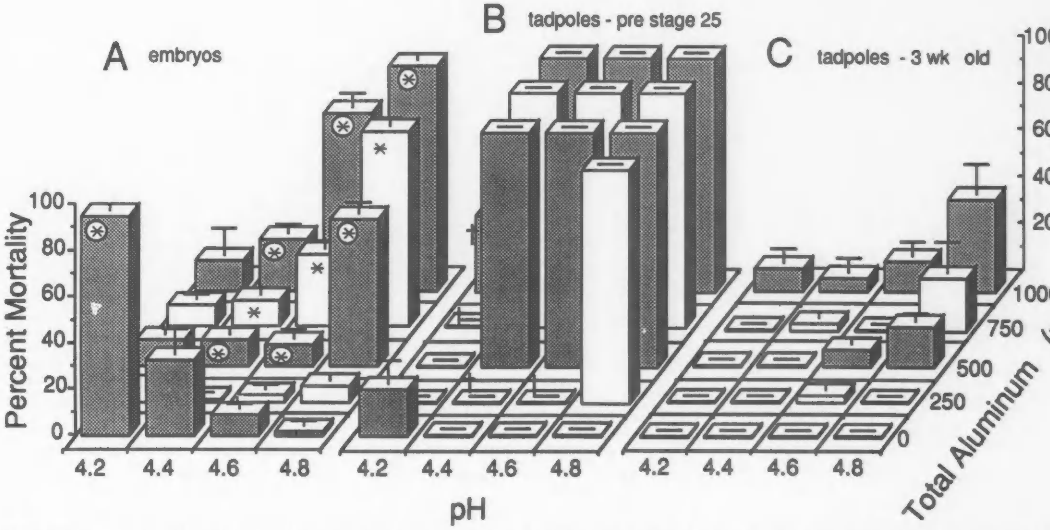

FIG. 1. Percent mortality of *Rana pipiens* embryos (A), prestage 25 tadpoles (B) and 3-wk old tadpoles (C) exposed to a range of pH and Al concentration. Values are means ± SE means ($n=30$ per replicate for embryos and $n=10$ per replicate for prestage 25 tadpoles and 3-wk old tadpoles; three replicates per treatment). Exposure periods were until hatching for embryos, until stage 25 for prestage 25 tadpoles (approximately 96 h) and 96 h for 3-wk old tadpoles. An asterisk (*) indicates the treatments where hatchlings (embryo test), were abnormal or dead, and crosses (+) indicate treatments where prestage 25 tadpoles were abnormal, could not swim, and did not reach stage 25. Mortalities of controls (pH 6.5 and no Al) were 1 ± 1, 0, and 0% for the three life stages, respectively.

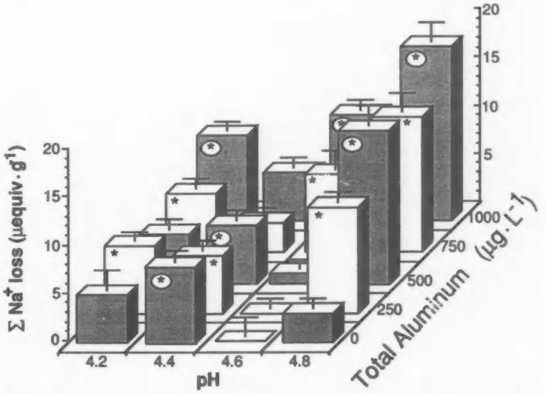

FIG. 2. Amount of body sodium lost (relative to controls) in 3-wk old *Rana pipiens* tadpoles which survived a 96 h exposure to a range of pH and Al concentration. Values are means ± SE means; $n=9$ or 10 except at pH 4.8 and 1000 $\mu g \cdot L^{-1}$ Al where $n=6$. An asterisk indicates a significant difference from control levels ($p<0.05$). Control body sodium at pH 6.5 and 0 $\mu g \cdot L^{-1}$ Al was 53 ± microequivalents$\cdot g^{-1}$.

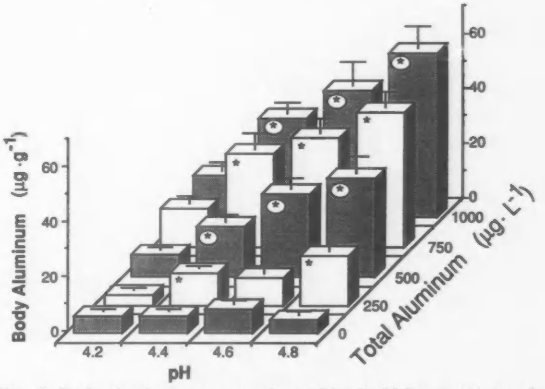

FIG. 3. Body aluminum concentrations of 3-wk old *Rana pipiens* tadpoles which survived a 96 h exposure to a range of pH and Al concentration. Values are mean ± SE means; $n=9$ or 10 except at pH 4.8 and 1000 $\mu g \cdot L^{-1}$ Al where $n=6$. An asterisk indicates a significant difference from control levels ($p<0.05$). Control body Al at pH 6.5 and 0 $\mu g \cdot L^{-1}$ was 8 ± 1$\cdot g^{-1}$.

1C), but statistically significant effects were still evident ($p<0.001$). Three-week old tadpoles were resistant to low pH with 0% mortality occurring at pH 4.2 and 0 $\mu g \cdot L^{-1}$ Al (control mortality at pH 6.5 ws 0%) Aluminum was generally without effect at pH 4.2 to 4.6 except for small increases in mortality (6–13%) at 1000 $\mu g \cdot L^{-1}$. Aluminum was most toxic at pH 4.8, but only 40% of tadpoles at 1000 $\mu g \cdot L^{-1}$ died. Seventy-eight percent of all mortality occurred within the first 24 h.

Sodium Loss in 3-wk old Tadpoles

Although mortality was relatively low in 3-wk old tadpoles, many of the surviving animals had lowered body sodium concentrations indicating sublethal stress (Fig. 2). This was most obvious in the three most toxic treatments (pH 4.8, 500, 750, and 1000 $\mu g \cdot L^{-1}$ Al) where body sodium concentration was reduced by 26 to 34% of initial. However, body sodium concentration was also reduced by 21% at pH 4.8, 250 $\mu g \cdot L^{-1}$ Al, where 0% mortality occurred. At pH 4.2 and 4.4 and over all Al concentrations, body sodium concentration was reduced by 11 ± 1%. The body sodium concentration of tadpoles removed

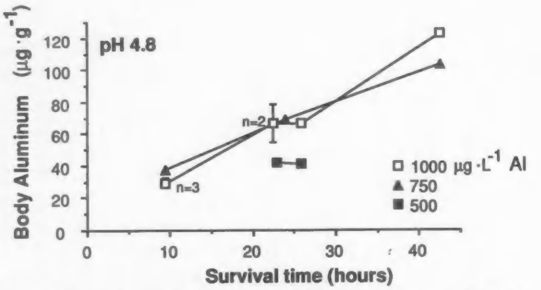

FIG. 4. Uptake of aluminum by 3-wk old *Rana pipiens* tadpoles killed by exposure to aluminum plotted against survival time. All animals were removed from exposure solutions at the time of death. Values are individual points except where indicated by standard error bars.

at death was 24 ± 1 ($n = 14$) microequivalents $\cdot g^{-1}$ wet mass, indicating a 55% loss of total body sodium.

Aluminum Uptake in 3-wk old Tadpoles

Aluminum uptake was positively related to pH and the external concentration of Al (Fig. 3). Although, Al uptake was correlated to the reduction in body sodium over all treatments ($r^2 = -0.64$, $n = 21$, $p < 0.05$), it was not necessarily an accurate indicator of the reduction of body sodium in specific treatments. For example, tadpoles took up relatively high levels of Al at pH 4.4, 750–1000 $\mu g \cdot L^{-1}$ and pH 4.6, 500 $\mu g \cdot L^{-1}$, yet body sodium concentrations were not significantly reduced. The body Al concentration of tadpoles at death (56 ± 8, $n = 14$) was much more variable than body sodium at death (24 ± 1) and the amount of Al accumulation was directly related to survival time (Fig. 4).

Discussion

Relative Toxicity of Low pH and Al to Different Life Stages

This is the first study to report the relative sensitivity of embryos, prestage 25 tadpoles, and 3-wk old tadpoles to acid and Al exposure. Mortality of embryos and prestage 25 tadpoles was directly related to both acidity and the concentration Al. However, embryos were more sensitive to low pH and prestage 25 tadpoles were more sensitive to Al. Three-week old tadpoles were relatively less sensitive to either low pH or Al. For embryos, Al toxicity was observed at pH's 4.6 and 4.8, while Al was actually protective against acid toxicity at pH 4.2 and 4.4. Clark and LaZerte (1987) were the first to report that Al can ameliorate the toxic effects of low pH on amphibian embryos. They found that increasing external Al from 0 to 200 $\mu g \cdot L^{-1}$ increased percent hatching in spotted salamander embryos (*Ambystoma maculatum*) by 6 to 13% at pH 4.3. Our toxicity tests using *R. pipiens* embryos confirm this initial observation, and demonstrate that the degree of protection can be much larger; mortality declined from 94 to 12% when Al was increased from 0 to 250 $\mu g \cdot L^{-1}$ at pH 4.2. Aluminum has also been shown to be protective to varying degrees against low pH in fish (Schofield and Trojnar 1980; Baker and Schofield 1982).

Our finding that prestage 25 tadpoles are the life stage most sensitive to Al is important because embryos or older tadpoles have been the only life stages examined in field assessments of the effects of acidic precipitation. The complete mortality or abnormal development which occurred at even the lowest concentration of Al tested (250 $\mu g \cdot L^{-1}$) at pH's 4.4, 4.6, and 4.8 indicates the need to include prestage 25 tadpoles in determinations of reproductive success of amphibians in acidified, metal contaminated ponds. At pH 4.2, Al was protective against acid toxicity in prestage 25 tadpoles, but less so than in embryos.

Three-week old tadpoles were more tolerant to low pH and Al than either embryos or prestage 25 tadpoles. Tolerance to low pH has been shown to increase with age, but it is not known whether this is due to a simple increase in size or developmentally related changes (Pierce et al. 1984; Freda and Dunson 1985a). Other studies have also documented the high tolerance of the tadpole stage to Al (Clark and LaZerte 1985; Cummins 1986). We could not demonstrate a protective effect of Al in 3-wk old tadpoles because no acid related mortality occurred. However, as was the case in embryos and prestage 25 tadpoles, the toxicity of Al was positively related to pH (highest at pH 4.8). Although mortality of 3-wk old tadpoles was low (<20%) in most experimental treatments, the addition of Al caused tadpoles to lose sodium, indicating sublethal stress in survivors.

Mechanisms of Low pH and Al Toxicity in Embryos

Our study substantiates the premise that embryos exposed to lethally acidic pH's display one of two characteristic toxic syndromes (Freda 1986). (1) At very low pH (4.2 in this study), embryos stopped developing shortly after initial exposure (referred to as early mortality). Although never fully studied, early mortality at very low pH's probably involves direct disruption of physiological and biochemical processes by H^+. (2) At higher but still lethal pH's (4.4 in this study) or when Al is present, embryos develop normally, but the vitelline membrane fails to expand forcing the elongating embryos to become tightly constricted. This syndrome has been referred to as the curling defect because of the characteristic appearance of the embryo. In this study, most curled embryos were unable to escape the vitelline membrane at hatching and eventually died. The exception was curled embryos at pH 4.2 and 250–1000 $\mu g \cdot L^{-1}$ Al, which evenutally did hatch.

The toxicological mechanisms which prevent hatching at low pH or elevated Al are complex and not understood. For example, H^+ or Al may inhibit the release of hatching enzyme which digests the vitelline membrane under normal circumstances (Katagiri 1976; Yoshizaki 1978), inhibit the activity of free hatching enzyme, somehow make the vitelline membranes more resistant to hatching enzyme, or disrupt the normal permeability characteristics of the vitelline membrane to ions and water. Probably more than one of these putative mechanisms is involved because depending upon the specific water chemistry, embryos with a similar degree of curling may or may not hatch (Freda and Dunson 1985a; Clark and LaZerte 1987; this study).

Embryos are probably more sensitive to low pH than prestage 25 tadpoles because moderate levels of acidity appear to specifically affect the hatching process and not the embryo itself. Dunson and Connell (1982) have shown that embryos will survive at normally lethal pH's if the vitelline membrane is removed. While vitelline membrane dysfunction is the cause of embryonic mortality at low pH and high Al levels, it may also be acting as a partial barrier to Al permeation. For example, embryos which survived at >500 $\mu g \cdot L^{-1}$ Al treatments (at pH 4.4 to 4.8) became swollen and died shortly after hatching (Fig.

1A), and prestage 25 tadpoles were more sensitive than embryos to Al (Fig. 1B).

Protective Effect of Al

The protective effect of Al against lethally acidic water is similar to that of calcium and magnesium (Freda and Dunson 1985a) and all three ions prevent early mortality at extremely low pH ($\leq$4.2). Calcium has the well known ability to reduce the permeability of biological membranes (Gordon and Sauerheber 1982; Levine and Williams 1982). Aluminum may similarly reduce the loss of electrolytes or prevent the uptake of H^+.

Qualitative differences in the way different amphibian species respond to Al also exist. Aluminum ameliorates low pH toxicity in both the spotted salamander (Clark and LaZerte 1987) and the leopard frog (this study). However, Al addition is not protective in the wood frog (*Rana sylvatica*) where it actually increases the toxicity of acidic water regardless of pH (Clark and LaZerte 1985; Freda et al. 1990). Calcium also prevents low pH induced mortality in leopard frog and spotted salamander embryos, but does not in wood frogs (Freda and Dunson 1985a; Dale et al. 1985b). Ion additions (calcium or Al) prevent early mortality in all three species, so the real difference in protection occurs at hatching. As hatching nears, all three species become curled, but only spotted salamanders and leopard frogs hatch while wood frogs remain trapped and die. A high concentration of calcium by itself ($\geq$10 $mg \cdot L^{-1}$) also promotes the curling defect at nonlethal pH's, and again spotted salamanders and leopard frogs eventually hatch, but wood frogs do not (Freda and Dunson 1985a; Dale et al. 1985b).

Aluminum Uptake in 3-wk old Tadpoles

Although fully developed tadpoles are not the most sensitive life stage to acidity or Al, mortality might occur during episodic changes in pond chemistry such as during large rainstorms. A reduction in growth rate resulting from chronic sublethal stress is a more likely scenario and may reduce larval survival (Freda 1986). It would be useful then to develop a method to assess the health of tadpoles in acidic metal contaminated ponds. We therefore measured Al uptake in tadpoles to test if it was a precise indicator of the level of Al exposure or the magnitude of physiological disruption. However, based on our results, we feel that body Al accumulation is too variable for useful predictions of exposure history or physiological status for two reasons. First, in some treatments, tadpoles accumulated Al without a concomitant decrease in body Na levels. Second, the level of Al uptake was positively related to exposure time and pH, so that measurements in waters experiencing episodes of low pH and high Al would be difficult to interpret. Our uptake experiments do, however, indicate something about the mechanisms of effect. Both Al uptake and mortality rose with increasing pH indicating that Al $(OH)_x$ may bind to or precipitate on biological membranes more easily than Al^{3+}, thus potentially increasing toxicity.

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Role of Organic Complexation in the Toxicity of Aluminum to *Rana pipiens* Embryos and *Bufo americanus* Tadpoles

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Freda, J., V. Cavdek, and D. G. McDonald. 1990. Role of organic complexation in the toxicity of aluminum to *Rana pipiens* embryos and *Bufo americanus* tadpoles. Can. J. Fish. Aquat. Sci. 47: 217–224

This study investigated the influence of naturally occurring organic compounds on the survival of amphibian embryos and larvae in acidic, aluminum contaminated water. A series of laboratory tests were conducted which measured aluminum toxicity in artificial soft water (ASW) diluted with varying amounts of pond water which contained dissolved organic compounds. At pH 4.5 for tadpoles of *Bufo americanus* and pH 4.8 for embryos of *Rana pipiens*, the organic compounds (DOC 5.7 to 16.2 $mg \cdot L^{-1}$) complexed the aluminum and thus increased the LC50 for total aluminum by more than two fold. At pH 4.2, 100% ASW and the four dilutions of pond water were toxic to *R. pipiens* embryos (75–96% mortality). In contrast to higher pH's, aluminum ameliorated acid toxicity which resulted in a 26% reduction in mortality in 100% ASW at 250 $mg \cdot L^{-1}$ total aluminum. Although the organic compounds in the pond water also complexed aluminum at pH 4.2, protective levels of labile aluminum (≥ 180 $\mu g \cdot L^{-1}$) were still present at 450 $\mu g \cdot L^{-1}$ total aluminum. However, at a given level of labile aluminum in pH 4.2 water, pond water was more toxic to embryos than ASW. At pH 4.2, pond water without added Al was also significantly more toxic to embryos than 100% ASW with 0 $\mu g \cdot L^{-1}$ Al. Toxicity tests using purified humic and fulvic acid sugested that these compounds may be the toxic agents in high dissolved organic carbon (DOC) pond water.

On étudie l'influence de composés organiques naturels sur la survie d'embryons et de larves d'amphibiens dans un milieu acide contaminé d'aluminium. On a effectué une série de tests expérimentaux pour quantifier la toxicité de l'aluminium en eau douce artificielle diluée avec diverses quantités d'eau d'étang contenant des composés organiques dissous. Au pH 4,5 chez les têtards de *Bufo americanus* et au pH 4,8 chez les embryons de *Rana pipiens*, les composés organiques (COD 4,7–16,2 $mg \cdot L^{-1}$) ont formé un complexe avec l'aluminium pour accroître la CL50 de l'aluminium total de plus de deux fois. Au pH 4,2, l'eau douce artificielle à 100 % et les quatre dilutions d'eau d'étang se sont révélées toxiques pour les embryons de *R. pipiens* (mortalité de 75 à 96 %). Par contraste au pH élevé, la présence d'aluminium a amplifié la toxicité de l'acide pour donner une baisse de 26 % du taux de mortalité en eau douce artificielle à 100 % quand la concentration totale d'aluminium s'élevait à 250 $mg \cdot L^{-1}$. Même si les composés organiques présents dans l'eau d'étang ont aussi formé un complexe avec l'aluminium au pH 4,2, des niveaux protecteurs d'aluminium instables (180 $\mu g \cdot L^{-1}$) étaient toujours présents à une concentration totale d'aluminium de 450 $\mu g \cdot L^{-1}$. Toutefois, à une teneur donnée d'aluminium instable au pH 4,2, l'eau d'étang était plus toxique pour les embryons que l'eau douce artificielle. Au ph 4,2, l'eau d'étang sans Al était aussi nettement plus toxique pour les embryons que l'eau douce artificielle à 100 % chargée de 0 $\mu g \cdot L^{-1}$ Al. Les résultats de tests de toxicité portant sur les acides humique et fulvique purifiées portent à croire que ces composés peuvent être les agents toxiques dans l'eau d'étang à teneur élevée de carbone organique dissous.

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Acidic conditions in ephemeral ponds can have dramatic, negative effects on the reproductive success of amphibians (see recent reviews by Pierce 1985; Freda 1986). The acidity may be anthropogenic in origin (e.g. acidic deposition, acidic mine drainage) or may be derived from natural sources (e.g. organic acids, sphagnum). Water with a low pH may be directly toxic to embryos and larvae and thus limit recruitment into the adult population. In addition, pH also influences the concentration of aluminum which may alter the water's toxicity. The solubility of aluminum is increased at low pH, causing its mobilization from surrounding soils and the pond's sediments. In our previous paper (Freda and McDonald 1990), we reported that at very low pH's (4.2–4.4), aluminum ameliorates the toxic effects of low pH on embryos of the leopard frog (*Rana pipiens*). However, at higher pH's (4.6–4.8), aluminum is toxic. The spotted salamander (*Ambystoma maculatum*) exhibits a similar pattern of response (Clark and LaZerte 1987), but other species may respond differently. For example, aluminum toxicity increases with decreasing pH for *Bufo americanus* (Clark and LaZerte 1985; Freda et al. 1990), *Hyla crucifer* (Dale et al. 1985), and *Rana temporaria* (Andren et al. 1988). Clark and LaZerte (1985) also found that aluminum toxicity was inversely related to water pH in *Rana sylvatica*, but

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TABLE 1. Ionic composition of artificial soft ater (ASW), Killarney pond water, and Luther pond water (N.D. = not detectable).

Chemical parameters	ASW	Killarney	Luther
pH	6.5	4.5	7.4
Na ($mg \cdot L^{-1}$)	2.5	4.7	0.3
K ($mg \cdot L^{-1}$)	0.6	1.9	0.2
Ca ($mg \cdot L^{-1}$)	1.3	5.4	12.0
Mg ($mg \cdot L^{-1}$)	0.7	1.2	3.5
Mn ($mg \cdot L^{-1}$)	N.D.	9	180
Ni ($\mu g \cdot L^{-1}$)	N.D.	23	N.D.
Pb ($\mu mg \cdot L^{-1}$)	4	N.D.	28
Fe ($mg \cdot L^{-1}$)	< .1	2.7	5.1
Cu ($\mu g \cdot L^{-1}$)	N.D.	14	15
Cd ($\mu g \cdot L^{-1}$)	8	N.D.	N.D.
Zn ($mg \cdot L^{-1}$)	N.D.	3	N.D.
Al (total $\mu g \cdot L^{-1}$)	2	92	118
Al (labile $\mu g \cdot L^{-1}$)	N.D.	4	N.D.
Cl ($mg \cdot L^{-1}$)	4.3	7.3	1.8
SO_4 ($mg \cdot L^{-1}$)	0.6	1.3	6.8
F ($mg \cdot L^{-1}$)	0.07	0.07	0.07
DOC ($mg \cdot L^{-1}$)	1.0	26	57
Color (true-units)	0	54	660
Tannin/lignin ($mg \cdot L^{-1}$ tannic acid)	N.D.	4.4	9.8
Absorption 400 nm	0	0.175	0.465

A dominant characteristic of many acidic breeding ponds of amphibians is their "dark water" resulting from high concentrations of naturally occurring organic acids (Gosner and Black 1957; Cook 1983; Karns 1983; Freda et al. 1990). Several studies on fish have conclusively demonstrated that organic molecules bind aluminum and thus make it biologically unreactive and nontoxic (Driscoll et al. 1980; Neville 1985; Hutchinson and Sprague 1987). Dissolved organic matter also binds other toxic metals (e.g. copper, cadmium), rendering them nontoxic (Zitko et al. 1973; Buckley 1983). Although an extensive literature exists describing the levels of dissolved organic matter and aluminum in amphibian breeding ponds, the toxicity of aluminum or the protection afforded by the organic molecules for amphibians is unknown (Freda 1986). Therefore it is important to characterize the effects of organic complexation on the protective or toxic action of aluminum before rigorous assessments of pond water toxicity can proceed. The situation is clouded further by the fact that an unknown component of darkly stained pond water is toxic to amphibian embryos (Dunson and Connell 1982; and Saber and Dunson 1978; Karns 1983; Freda and Dunson 1986).

The objective of this study was to determine if the levels of dissolved organic compounds typically found in dark water ponds can significantly reduce toxicity of aluminum to amphibians. We also conducted a toxicity test with purified humic and fulvic acid to determine if it produces the same toxic response in amphibian embryos as pond water with a high concentration of dissolved organic compounds. In addition, we fractionated aluminum in exposure solutions to determine if toxicity could be predicted by levels of labile (free) aluminum.

Methods and Materials

Animals

Leopard frog (*Rana pipiens*) embryos were obtained by artificial fertilization as described by Rugh (1962). A more detailed description may be found in Freda and McDonald (1990). Tadpoles of the american toad (*Bufo americanus*) were reared from a locally collected egg mass. All tadpoles were maintained in artificial soft water (ASW, Table 1) at room temperature (20°C) and ambient lighting, and fed commercial trout food. Tadpoles were fasted one day prior to and during experiments to reduce pH drift and organic complexation of aluminum by feces.

Water Chemistry

Experimental solutions were made by mixing varying amounts of ASW and natural water. ASW was made by the dilution (1:40) of dechlorinated tap water with ion free water from an ion exchange column. Pond water was collected from two locations with very different geochemical characteristics. Luther pond (Luther Conservation Area, Dufferin Co., Ont.) is a minerotrophic fen with high concentrations of calcium and extremely dark water (Table 1). Killarney pond is a low pH, dark water, ephemeral pond within Killarney Provincial Park (Killarney, Ont., Table 1) and is characteristic of most ponds of this region. These two very different sites were selected for water collection to test if general predictions concerning amelioration of aluminum toxicity could be made regardless of water type. All pond water was stored at 4°C until use.

Varying amounts of $NaC1$, $KC1$, $CaC1_2$, and $MgC1_2$ were added to the different dilutions of ASW and pond water so the concentrations of Na, K, Ca, and Mg were 4, 1, 4, and 1 $mg \cdot L^{-1}$, respectively, in each cell of the experimental matrix. Chloride did vary slightly between cells, but its concentration did not approach levels needed to influence toxicity (Freda and Dunson 1985a). The concentration of aluminum was manipulated by the addition of varying amounts of an $AlCl_3$ stock solution. Killarney and Luther pond water did contain some native aluminum (Table 1), but all was organically complexed (nonlabile).

The pH of experimental solutions was checked twice daily with a Markson model 88 pH meter and Cole Palmer combination electrode and readjusted to the desired pH with dilute H_2SO_4. In all experiments, pH drift never exceeded 0.07 units in any experiment and did not exceed 0.02 units in solutions with a $pH \leq 4.5$.

The aluminum concentration of the water was measured at the start and the end of experiments by the catechol-violet method (Dougan and Wilson 1974; Seip et al. 1984). Aluminum was fractionated using an ion exchange column method (Driscoll 1984) where the ion exchange resin (Amberlite IR-120, Na form) binds labile (free) aluminum. Aluminum measurements on untreated water detect total monomeric aluminum, while measurements on the column effluent detect only nonlabile (complexed) aluminum. Labile monomeric aluminum is arrived at through subtraction.

Total monomeric aluminum measured in 100% ASW solutions was generally within 5% of nominal concentration. However, total monomeric aluminum in solutions containing pond water was slightly higher because of the native aluminum present. The exact percent increase over nominal levels ranged from 0.06% (in 10% Luther with 2000 $\mu g \cdot L^{-1}$ Al) to 36% (in 60% Killarney with 150 $\mu g \cdot L^{-1}$) and was dependent on pond water type, its dilution, and the amount of nominally added aluminum. Most of the native aluminum in unaltered pond water was complexed, but some dissociation did occur when pH was lowered. However, the increase in labile aluminum was small relative to the experimental addition ($\leq 50\ \mu g \cdot L^{-1}$). Therefore, we will report nominal concentrations for total monomeric aluminum and measured values for labile aluminum. At pH 4.8, the concentration of total monomeric aluminum at 250 and 500 $\mu g \cdot L^{-1}$ increased by 3–5% after 96 h due to evaporation, while it droped by 3–5% at 750 and 1000 $\mu g \cdot L^{-1}$. At pH 4.2 and 4.5, the concentration of total monomeric aluminum (at $\leq$1000 $\mu g \cdot L^{-1}$) also increased by 3–7%. However, at 1500 and 2000 $\mu g \cdot L^{-1}$ total monomeric aluminum (pH 4.5), its concentration was reduced by approximately 9% and 10–20%, respectively. This was caused by the precipitation of the organo-aluminum complexes between the 24th and 36th h of exposure, resulting in a decline in dissolved organic carbon (DOC) and nonlabile aluminum, but had no effect on labile aluminum. In all other experimental solutions, the ratio of nonlabile to labile aluminum did not change during the experimental period (96 h).

We made measurements of major cations (Na, K, Ca, Mg) and trace metals (Cu, Cd, Zn) by atomic absorption spectrophotometry (Varian model 1275). Tannin/lignin content (expressed as milligrams per litre tannic acid) was measured with HACH test kit (HACH 1975). Other analyses shown in Table 1 were performed by the Ontario Ministry of the Environment (Rexdale).

Toxicity of aluminum to embryos

Rana pipiens embryos ($n = 30$ at pH 4.2, $n=20$ at pH 4.8, three replicates) were placed in test chambers 3 h after fertilization (2–4 cell stage; stage 3–4, Gosner 1960), which held 1 L of water (described in Freda and McDonald 1990). Embryos were exposed to a range of aluminum (0 to 450 $\mu g \cdot L^{-1}$ at pH 4.2 and 0 to 1000 $\mu g \cdot L^{-1}$ at pH 4.8) in 100% ASW, 30 and 60% Killarney pond water, and 10 and 20% Luther pond water. These dilutions were chosen based on absorbance (at 400 nm) measurements so that 30 and 60% Killarney pond water would contain similar levels of organic compounds as in 10 and 20% Luther pond water. Each day until hatching which occurred 4 d after fertilization, the number of living and dead embryos were recorded and qualitative descriptions of abnormalities were noted. Dead embryos did not promote fungus growth and were not removed.

Toxicity of Humic and Fulvic Acid to Embryos

Rana pipiens embryos ($n=30$, one replicate) were exposed to seven concentrations of humic or fulvic acid (0, 10, 20, 30, 40, 50, 60 $mg \cdot L^{-1}$) at two different pH levels (4.4 and 6.5). Humic and fulvic acid were obtained from the International Humic Acid Substances Society (IHASS peat humic acid reference 1R103H; IHASS nordic aquatic fulvic acid reference 1R105F). The humic and fulvic acid was 50% carbon by weight (IHASS, pers. comm.).

Toxicity of Aluminum to Tadpoles

Three-week old (stage 26, Gosner 1960) *B. americanus* tadpoles ($n=10$, three replicates) were exposed to a range of aluminum (0 to 2000 $\mu g \cdot L^{-1}$) in five dilutions of Luther pond water (0 to 20%) at pH 4.5. While concentrations of aluminum in excess of 1000 $\mu g \cdot L^{-1}$ are generally not considered environmentally realistic, we tested these high concentrations so that we could precisely determine the LC50 for aluminum. Death was defined as the lack of response to mechanical stimuli and dead tadpoles were removed. Toxicity tests lasted for 96 h, and in most experiments, $\geq$95% of the mortality occurred within the first 24 h.

TABLE 2. Percent mortality of *R. pipiens* embryos (from fertilization to hatching) at pH 4.2 over a range of aluminum in 100% artificial soft water (ASW) and in different dilutions of pond water from two locations. All values are means ±SEM ($n=30$, three replicates).

	Total aluminum ($\mu g \cdot L^{-1}$)			
Water	0	125	250	450
100% ASW	75±8	60±7	49±6	54±7
30% Killarney	78±4	64±5	58±3	57±10
60% Killarney	96±5	87±6	75±2	82±3
10% Luther	87±2	91±2	78±1	72±6
20% Luther	94±3	100	92±1	89±3

Statistical Analysis

All data are reported as means ±1 SE of the mean (SEM). The LC50 and 95% confidence interval for aluminum at each dilution of pond water were calculated using measured values for total monomeric aluminum by the moving average method (Stephan 1977; Peltier and Weber 1985). Percent mortality data were compared using two sample *t*-tests ($p<0.05$) after arcsine square root transformation (Steel and Torrie 1960).

Results

Toxicity of Low pH and Aluminum to Embryos in 100% ASW

Embryos of *R. pipiens* suffered high mortality (75%) in 100% ASW at pH 4.2 without aluminum (Table 2), whereas pH 4.8 ASW without aluminum was nontoxic (5% mortality, Table 3). Aluminum was toxic only at pH 4.8 and the LC50 for 100% ASW was 471 $\mu g \cdot L^{-1}$. At pH 4.2, aluminum ameliorated the toxic effects of the acid water which resulted in a 26% decline in mortality at 250 $\mu g \cdot L^{-1}$ (Table 2). Given this complex pattern of toxicity, organic complexation of aluminum could theoretically increase or decrease water toxicity depending on the pH.

Toxicity of Humic and Fulvic Acid to Embryos

The humic and fulvic acid increased the mortality (Table 4) of *R. pipiens* embryos at pH 4.4, but was without effect at pH 6.5. The LC50 (and 95% CI) for humic and fulvic acid in pH 4.4 water was 15.6 (13.3–19.2) $mg \cdot L^{-1}$ and 14.1 (4.8–18.1) $mg \cdot L^{-1}$, respectively. LC50 values for humic and fulvic acid in pH 6.5 water could not be calculated because mortality was not correlated to the concentration of either organic acid. At pH 4.4, both humic and fulvic acid stained the egg jelly and membranes a dark brown color and caused these structures to become "tough and rubbery." The embryos became tightly curled within the egg membranes and were unable to hatch. These effects were not seen at pH 6.5.

Toxicity of Pond Water to *Rana pipiens* Embryos

Exposure of *R. pipiens* embryos to various dilutions of either Killarney (60%) or Luther pond water (10 and 20%) at pH 4.2 (0 $\mu g \cdot L^{-1}$ Al) significantly increased mortality as compared with 100% ASW (Table 2). Similar to the humic and fulvic acid tests, embryos in pH 4.2 pond water were unable to hatch from their egg membranes and jelly which were stained, tough and rubbery. All dilutions of pond water (at 0 $\mu g \cdot L^{-1}$ Al) were not toxic at pH 4.8. As discussed later, the toxicity of our pond water may be attributable to the high levels of dissolved organic

TABLE 3. Percent mortality of *R. pipiens* embryos (from fertilization to hatching) at pH 4.8 over a range of aluminum and in 100% artificial soft water (ASW) and in different dilution of pond water from two locations. Percent mortality values are means ± SEM ($n=20$, three replicates) and the 95% CI is given for LC50 values.

	Total aluminum ($\mu g \cdot L^{-1}$)					
Water	0	250	500	750	1000	LC50
100% ASW	5±3	12±10	52±5	91±2	94±3	471 (404–621)
30% Killarney	3±2	3±2	10±4	15±5	42±10	> 856
60% Killarney	10±3	8±2	9±2	13±5	17±6	> 1001
10% Luther	4±4	7±5	4±2	9±3	22±1	> 980
20% Luther	9±5	5	20±3	11±3	28±5	> 1018

TABLE 4. Percent mortality (from fertilization to hatching) of *Rana pipiens* embryos exposed to a range humic or fulvic acid concentration at two pH levels. All values ae mean ± SEM ($n=30$, one replicate).

pH	Concentration ($mg \cdot L^{-1}$)	Humic acid (% mortality)	Fulvic acid (% mortality)
6.5	0	10	7
	10	20	17
	20	10	13
	30	7	10
	40	13	13
	50	13	10
	60	0	17
4.4	0	20	30
	10	17	40
	20	70	60
	30	73	77
	40	87	83
	50	93	77
	60	97	90

compounds which include humic and fulvic acid. This makes interpretation of our results more difficult because the very compounds which bind aluminum, rendering it nontoxic, may become toxic themselves at low pH. However, our goal was to test the ability of "natural water" to ameliorate aluminum toxicity so the confounding effect of the toxicity of organic compounds, while unavoidable, is nonetheless realistic.

Organic Complexation of Aluminum at pH 4.2–*Rana pipiens* Embryos

As previously stated, aluminum is protective against acid toxicity to *R. pipiens*. Therefore it was of interest to us to test if organic complexation reduced the protective effect of aluminum. Increasing the concentration of total aluminum to 125 $\mu g \cdot L^{-1}$ in 100% ASW ameliorated acid toxicity (15% reduction in mortality) and this protection leveled off between 250 and 450 $\mu g \cdot L^{-1}$ (21 to 26% reduction in mortality, Table 2). In 30% Killarney pond water, the addition of aluminum had a similar protective effect and although organic complexation reduced the amount of labile aluminum, levels were still high enough (106–323 $\mu g \cdot L^{-1}$) to be protective (Fig. 1). In 60% Killarney pond water and 10% Luther pond water, the addition of aluminum reduced mortality, but not to the degree achieved in 100% ASW (Table 2). Aluminum addition was less protective even though levels of labile aluminum at 450 $\mu g \cdot L^{-1}$ total aluminum were 274 and 281 $\mu g \cdot L^{-1}$, respectively. This may reflect the intrinsic toxicity of high DOC pond water because the egg membranes became more stained and rubbery as the concentration of pond water was increased. In 20% Luther pond water the staining of the egg membranes was the greatest and the addition of aluminum had no protective effect (Table 2) even though 180 $\mu g \cdot L^{-1}$ labile aluminum was present (Fig. 1). In 100% ASW, at all concentrations of aluminum, embryos died early during development (i.e. between yolk plug stage and neurulation). In contrast, when exposed to the various dilutions of pond water (at all aluminum concentrations), embryos died of the curling defect.

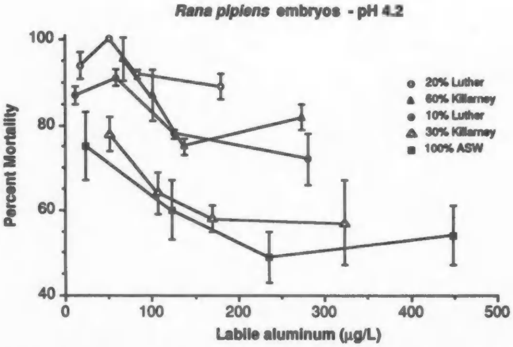

FIG. 1. Percent mortality of *R. pipiens* embryos at pH 4.2 plotted against labile aluminum concentration. The percent mortality data were taken from Table 2.

Organic Complexation of Aluminum at pH 4.8 — *Rana pipiens* Embryos

In 100% ASW at pH 4.8, aluminum was toxic at concentrations ≥ 500 $\mu g \cdot L^{-1}$ (Table 3). Mortality was reduced in all

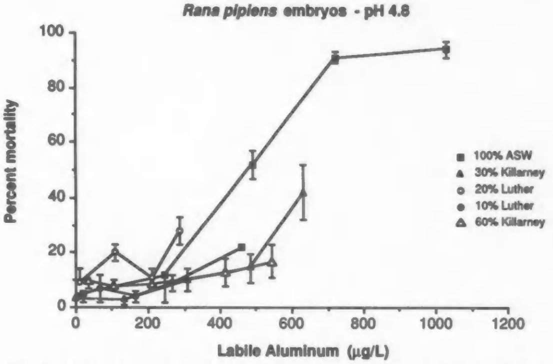

FIG. 2. Percent mortality of *R. pipiens* embryos at pH 4.8 plotted against labile aluminum concentration. The percent mortality data were taken from Table 3.

pond water treatments which resulted in a more than two-fold increase in the LC50 for aluminum. The LC50 values for aluminum in pond water are listed in Table 3 as greater than the highest concentration of total aluminum tested because mortality never exceeded 50%. Although the reduction in mortality was most likely caused by the complexation of aluminum, the measured concentration of labile aluminum was a poor predictor of mortality (Fig. 2). For example, 60% Killarney pond water with a labile aluminum concentration of 544 $\mu g \cdot L^{-1}$ caused 17% mortality, whereas 100% ASW with 491 $\mu g \cdot L^{-1}$ labile aluminum caused 52% mortality. In all cases except 20% Luther water, mortality in pond water was less than in 100% ASW at a specific concentration of labile aluminum (Fig. 2).

Organic Complexation at pH 4.5–*Bufo americanus* Tadpoles

The 96 h LC50 for *B. americanus* tadpoles at pH 4.5 was 627 $\mu g \cdot L^{-1}$ total aluminum (Table 5). However, increasing Luther pond water from 5 to 20% significantly reduced aluminum toxicity such that the LC50 for total aluminum increased to above 2000 $\mu g \cdot L^{-1}$. In addition, as was the case for embryos, the measured concentrations of labile aluminum were not good predictors of mortality (Fig. 3). Unlike its effect on *R. pipiens* embryos at pH 4.2, Luther pond water was not toxic to *B. americanus* tadpoles at pH 4.5.

Discussion

Reduction in Metal Toxicity by Organic Complexation

This study clearly demonstrates that low levels of DOC can greatly suppress aluminum toxicity. The addition of only 5.7 $mg \cdot L^{-1}$ DOC, in 10% Luther pond water, increased the LC50 for aluminum from 471 to above 980 $\mu g \cdot L^{-1}$ total aluminum for *R. pipiens* embryos at pH 4.8 (Table 3). Field surveys of acidic ponds (pH 4.0 to 5.0) have found that total aluminum generally ranges from 200 to 600 $\mu g \cdot L^{-1}$, although some ponds may contain levels as high as 1000 $\mu g \cdot L^{-1}$. A summary of the pH, DOC, and aluminum values reported by these surveys is presented in Table 6. These chemical surveys in conjunction with our laboratory data predict that aluminum would not be toxic to *R. pipiens* embryos in most breeding ponds with a high DOC. Most other species of amphibians are more tolerant of aluminum than *R. pipiens* and thus they are even less likely to suffer aluminum toxicity in dark water (Freda 1990). Tadpoles are more tolerant of aluminum than embryos, and as a result, environmental concentrations of aluminum rarely reach lethal levels even in low DOC ponds. For example, the LC50 (96 h) for *R. pipiens* tadpoles at pH 4.8 in 100% ASW is > 1000 $\mu g \cdot L^{-1}$ (Freda and McDonald 1990), and the LC50 (to metamorphosis) for *Rana temporaria* at pH 4.4 is 1600 $\mu g \cdot L^{-1}$ (Cummins 1986).

Water from the two ponds differed greatly in chemistry, yet both produced a large reduction in aluminum toxicity at environmentally realistic DOC levels (5.7 to 15.6 $mg \cdot L^{-1}$). However, water from the two sites did vary in its ability to complex aluminum and reduce toxicity. The fractionation of aluminum in the pond water dilutions revealed that, when diluted to a similar DOC level, Luther pond water bound more aluminum than Killarney pond water (Fig. 2). As a result, the toxicity of Al in 10% Luther water ($DOC = 5.7\ mg \cdot L^{-1}$) and 60% Killarney water ($DOC = 15.6\ mg \cdot L^{-1}$) at pH 4.8 were not significantly different (Table 3).

Toxicity of Dark Water

Evidence has been mounting that "acidic dark water" is more toxic than "clear water" with a similar pH. Dunson and Connell (1982) reported that the critical and lethal pH for embryos of *Xenopus laevis* were 0.4 pH units higher in high DOC bog water as compared with clear creek water. *Bufo woodhousei, Hyla andersoni,* and *Rana clamitans* also suffered higher mortality in high DOC pond water as compared with ASW at the same pH (Freda and Dunson 1986). Mortality of embryos transplanted into low pH (<5.0), high DOC ponds was generally higher than in clear water ponds or laboratory solutions with similar levels of acidity and aluminum (Freda and Dunson 1986; Freda et al. 1990). Field surveys have also found strong correlations between DOC and the abundance of amphibians (Clark and Hall 1985; Gascon and Planas 1986). However, because DOC is frequently correlated to pH and the concentration of toxic metals, these data must be interpreted cautiously. In most of the studies mentioned above, the chemistry of the exposure solutions were not rigorously defined. It is well known that humic compounds in dark waters act as a sink for toxic metals which may contribute to water toxicity (Reuter and Perdue

TABLE 5. Percent mortality of *B. americanus* tadpoles exposed to a range of aluminum at pH 4.5 in 100% artificial soft water (ASW) and in different dilutions of Luther pond water for 96 h. Percent mortality values are means ± SEM ($n = 10$, three replicates) and the 95% CI is given for LC50 values.

Water	0	500	750	1000	1500	2000	LC50
100% ASW	0	13 ± 12	83 ± 12	100	100	100	627 (588–672)
5% Luther	0	0	7 ± 3	87 ± 3	100	100	859 (824–899)
10% Luther	0	0	0	0	60 ± 26	90 ± 10	1379 (1300–1464)
15% Luther	0	0	0	0	10 ± 6	60 ± 25	1663 (1561–1859)
20% Luther	0	0	0	0	0	17 ± 12	> 1762

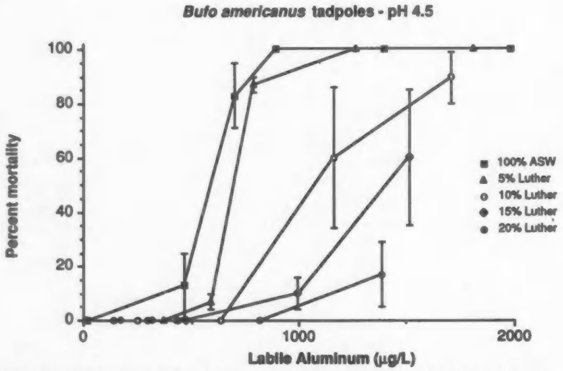

FIG. 3. Percent mortality of *B. americanus* tadpoles at pH 4.5 plotted against labile aluminum concentration. The percent mortality data were taken from Table 5.

1977). The concentrations of copper, cadmium, and zinc in all dilutions of Luther and Killarney pond water were below toxic levels for amphibians tested in clear water (0 mg·L^{-1} DOC; Freda 1990). Therefore, it is unlikely that these metals contributed to the toxicity of our high DOC pond water. No study has yet examined the toxicity of Mn or Ni to amphibians, but the levels in our pond water were well below toxic levels reported for fish (16 to 19 mg·L^{-1}, respectively, Lewis 1978; Brown 1968). Killarney and Luther pond water did contain high concentrations of iron but several studies on amphibians report no toxic effects at levels equal to or exceeding iron levels in our pond water (Cooke and Frazer 1976; Porter and Hakanson 1976; Beebee and Griffin 1977; Albers and Prouty 1987; and Freda et al. 1990).

Our finding that purified humic and fulvic acid are toxic to amphibian embryos strongly suggests that the humic compounds native to high DOC bogs and ponds may themselves be toxic. If one considers that 50 to 80% of DOC in natural water is composed of humic substances and that humic and fulvic acids are 50% carbon by weight (MacCarthy and Suffet 1989), then the concentration of humic material in amphibian breeding ponds with a DOC of 30 mg·L^{-1} (Table 6) would range from 30 to 48 mg·L^{-1}. Therefore, natural levels of humic and fulvic acid may be toxic because the incipient lethal level of these organic acids is between 10 and 20 mg·L^{-1} (Table 4). The DOC concentrations of 60% Killarney water and 20% Luther water were 15.6 and 11.4 mg·L^{-1} and both waters adjusted to pH 4.2 were more toxic than pH 4.2 ASW (Table 2). Humic material in surface waters is 55 to 90% fulvic acid, while the remainder is humic acid (MacCarthy and Suffet 1989; McKnight et al. 1985). In addition, the pattern of toxicity to humic and fulvic acid was qualitatively identical to that observed when aquatic animals are killed by high DOC pond water in two major ways. First, toxicity is inversely related to pH. In this study, humic and fulvic acid were toxic at pH 4.4, but not at pH 6.5 (Table 4), while Luther and Killarney pond water was more toxic than ASW at pH 4.2, but not at pH 4.8. Freda et al. (1990) also reported that *R. sylvatica* and *B. americanus* embryos could not hatch in dark water ponds (DOC>5 mg·L^{-1}) with a pH less than 5.0, but they could hatch at identical pH levels in clear water, or in dark water ponds if the pH was greater than 5.0. Petersen et al. (1986) demonstrated that maple leaf leachate and natural bog water significantly reduced growth and survivorship in shrimp (*Gammarus pulex*) and blackfly larvae (Diptera: *Simuliidae*). Similar to our findings, the toxicity of their test solutions was also inversely related to pH. Lowering the pH of high DOC water is thought to increase its toxicity through dissociation of "ionizable toxic components" (i.e. organic molecules, Petersen et al. 1986). Second, the appearance of amphibian eggs killed by humic acid and high DOC pond water is similar. The egg jelly and membranes become darkly stained, tough and rubbery, preventing the escape of the embryo (Gosner and Black 1957; Karns 1983; Freda and Dunson 1986; Freda et al. 1990). This may be the result of cross linking by the organic molecules. In agreement with Freda and Dunson (1985b), dark water was not toxic to tadpoles.

Several additional factors may also have contributed to the intrinsic toxicity of the dark waters used in this study, but we feel these can be discounted. (1) Although the pond waters did contain 90 to 110 µg·L^{-1} aluminum, it probably was not toxic because its concentration was too low, most was organically complexed, and lowering the pH should have decreased rather than increased its toxicity. (2) Calcium has been shown to ameliorate acid toxicity in amphibian embryos (Freda and Dunson 1985b). Organic compounds may bind calcium thus increasing the toxicity of acidic water. However, lowering the pH would theoretically dissociate calcium-organic complexes, thereby increasing its concentration. (3) The acidification of pond water may have released toxic amounts of CO_2. This probably was

TABLE 6. Chemical characteristics (mean ± SE and range) of amphibian breeding ponds from different geographic regions of North America. Note: ponds were not selected randomly in all areas so values may not be representative for that region.

Location	No. ponds	pH	Total Al	Labile Al	DOC	Color	Tannin/lignin	Reference
Ontario	6	5.322 ± 0.74	97 ± 85	31 ± 26	5 ± 4	—	—	Clark and Hall 1985
		4.41–6.29	7–210	1–57	2–10		—	
Ontario	20	5.64	154 ± 16	19 ± 3	8 ± 1	—	—	Clark 1986
		4.55–6.37	15–42	81–69	2–33	—	—	
Quebec	12	5.65 ± 0.21	93 ± 23	13 ± 4	13 ± 2	—	—	Gascon and Planas 1986
		4.31–6.77	13–295	0–51	3–30	—	—	
Pennsylvania	12	4.95 ± 0.23	202 ± 49	—	—	—	1.3 ± 0.2	Freda and Dunson 1986
		4.24–7.06	20–600	—	—	—	0.4–2.6	
New Jersey	9	4.43 ± 0.17	326 ± 64	—	—	—	2.5 ± 0.7	Freda and Dunson 1986
		3.91–5.34	110–740	—	—	—	0.6–7.5	
Virginia	10	4.30 ± 0.12	341 ± 122	—	—	64 ± 7	—	Albers and Prouty 1987
		3.66–5.18	809–1380	—	—	17–93	—	
Ontario	16	4.92 ± 0.14	364 ± 64	220 ± 67	12 ± 2	83 ± 80	7 ± 6	Freda et al. 1990b
		4.15–6.77	31 – 1155	1 – 1073	4 – 30	5 – 375	1 – 27	

not a factor because we aerated our solutions after acidification and most mortality occurred at hatching, 4 d after acidification.

Prediction of Water Toxicity

To predict the negative impact of anthropogenic acidification (i.e. acid rain and mine drainage) or the influence of natural acidity on amphibian populations, precise estimates of water toxicity are needed. In most studies on fish, the toxicities of metals (aluminum and copper) were closely related to the levels of "free" or uncomplexed metal (Zitko 1973; Hutchinson and Sprague 1987). In our study, it appeared that mortality was reduced far beyond that expected by the reduction of labile aluminum alone (Fig. 1 and 2). Two possible explanations are that: (1) our measurements over-estimated the levels of labile aluminum, or (2) that the organics contained in dark water actually reduced the toxicity of the remaining labile aluminum. All aluminum fractionation techniques are operationally defined and do not discriminate between the different forms of aluminum based on biological availability. For example, weakly bound organo-aluminum complexes may not be toxic to amphibians, but may be broken apart by passage through the ion exchange column, thus inflating estimates of labile aluminum. In addition, the dissolved organic compounds may have had a direct effect on the response of embryos to aluminum. The staining of the eggs was clear evidence that the organic compounds were binding to the embryonic membranes. The organics may have competed with aluminum for binding sites or influenced vitelline membrane permeability. Regardless of the exact reason, it is clear that estimates of labile aluminum obtained by the ion exchange column method are not good predictors of pond water toxicity to amphibians where DOC levels exceed $5.7\ \mathrm{mg \cdot L^{-1}}$.

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LETTERS AND COMMENTS/ LETTRES ET COMMENTAIRES

What is Reflected by Otolith Size at Emergence ? — A Reevaluation of the Results in West and Larkin (1987)

Backcalculation of fish size from otolith microstructures is a relatively new praxis (for a review see Campana and Neilson 1985) and optimal procedures for attaining unbiased estimates of fish size from a catch population have not yet been developed.

In a recent paper, West and Larkin (1987) studied the fry to smolt stage, size-selective mortality of the Babine Lake population of sockeye salmon (*Oncorhynchus nerka*) in relation to backcalculated fork length at emergence. They concluded that the population was strongly affected by size-selective mortality at some later fry stage, and that mortality was determined by the alevin size at emergence. Although I do not disagree that size selection affected the later stage fry, I find it highly improbable that the results indicate a direct effect of emergence size alone on later survival.

West and Larkin's (1987) procedure can be described in two phases: first, they backcalculated fish length at emergence from survivors at several sampling occasions later in the life history. Linear (ln–ln) regressions were used with a correction for size assuming that an individual constant deviation from the common regression at the catch stage could be applied at the target stage analogous to the proportional deviation model (Carlander 1981). They then compared the backcalculated size-distributions with the observed distribution at emergence. Secondly, the data did not show size-selective effects during the period from emergence to the first sampling occasion following migration of the young salmon to Babine Lake in July. Therefore, the authors used a polynomial regression equation to backcalculate fork length at up to 20 d preceding the first sampling in the lake, to show that a ranked divergence of growth rates maintained a hierarchical size structure in the population. It is not clear whether the proportional deviation model was applied in this instance nor whether estimated size at the earlier time-point was compared with actual or estimated size at sampling.

The methods used for backcalculations are of fundamental importance when inferring shifts in the size distribution of a target population.

In the case of West and Larkin (1987), a bias was introduced in assuming that the individual deviations from the ln–ln transformed regression line were retained constant when a size-selective mortality was claimed. The bias is derived from the fact that slow growing individuals develop a body length — otolith relationship of lower slope than fast growing fish (Templeman and Squires 1957; Marshall and Parker 1982; Mosegaard et al. 1988; Secor and Dean 1989; Reznick et al. 1989). Thus, shifting the calculated regression line upwards in relation to the true line overestimated fish sizes at the emergence stage, whereas the size-selection may have actually occurred at a much later stage.

These observations, however, do not influence the very clear result of a shift towards greater otolith lengths at emergence among salmon which survived to the smolt stage. This result is so remarkable, considering the low correlation between fork length and otolith length at emergence, that a very high selective-mortality of fry with lesser fork lengths would be necessary to bring about the observed shift in otolith lengths. Calculations from some hypothetical size-selection events cast light on this problem.

West and Larkin (1987) reported fry to smolt survival of salmon with otolith sizes below and above the mean length (458.1 μm) of 8.9 and 63.6%, respectively, whereas the estimated survival of fish below and above mean fork length (29.55 mm) was 27.2 and 43.4%, respectively. They ascribed this discrepancy partly to inaccuracies in the backcalculation procedure.

West and Larkin (1987) claim that a higher selective mortality of fry with lesser fork lengths at emergence led to the observed shift in mean otolith length at emergence. This claim can be tested by comparing the observed shift with simulated shifts in mean otolith length at emergence. Simulations should predict what effect specific survival patterns, based on fork length, would have on mean otolith length at emergence.

A reconstruction of the fork length — otolith length data of the fry population at emergence may be conducted by drawing random observations from the data published in figure 6 (lower panel) and table 3 in West and Larkin (1987).

Effects of Simulated Size-selection on Otolith Length Distribution

I analysed the effects of different patterns of size-selective mortality on simulated fry populations. The fork length and otolith length distributions were reconstructed to simulate the pooled populations of sockeye fry as reported in West and Larkin (1987). The selective mortality exerted on proportions of fry with lesser fork lengths was manipulated to produce various positive shifts in mean otolith length at emergence. The least shift in fork length that would produce the observed shift in otolith mean length (493.6 μm) was estimated along with the corresponding total survival of the population.

A random number generator was used to calculate otolith total lengths (OTL) at emergence according to measurements from West and Larkin (1987, figure 6, lower panel) with the probability distribution stated in Table 1. One lower and three upper otolith length classes were added to the distribution indicated in figure 6, all populated minimally with 0.001. This was done to prevent too narrow a range of fork lengths which would in itself restrict the maximum shift in otolith length by a hypothetical size-selection. This precaution can thus be regarded as conservative to the null hypothesis.

From the regression analysis of ln fork length on ln OTL, residuals were stated to be normal and homogeneously distributed. Therefore, the statistics from West and Larkin (1987, table 3, Main lake column) were used to obtain a random sample of 10 000 pairs of data points of fork length versus otolith total length at emergence.

TABLE 1. Frequencies of otolith total lengths derived by measuring heights of bars in West and Larkin (1987, figure 6, lower panel), and adding several length classes with a low frequency of 0.001.

Median (class) otolith									
Length (μm)	337.5	352.5	367.5	382.5	397.5	412.5	427.5	442.5	
Frequency	0.001	0.004	0.009	0.014	0.023	0.050	0.082	0.215	
Length (μm)	457.5	472.5	487.5	502.5	517.5	532.5	547.5	562.5	577.5
Frequency	0.153	0.198	0.156	0.054	0.026	0.008	0.005	0.001	0.001

The respective fork lengths (FL) were calculated according to the following formula:

$$\mathrm{FL} = e^{1.52293 + 0.30493 \ln(\mathrm{OTL}) + \mathrm{RANNOR}(0.03717)),}$$

where RANNOR(std) is a function which produces random, normally distributed numbers with a mean equal to zero and standard deviation equal to 0.03717 ($S_{y \cdot x}$ in table 3, West and Larkin 1987).

The simulated data were not tabulated; however, various statistical analyses showed a close correspondence with the published data in West and Larkin (1987) (table 3, and figures 6 and 7, lower panels) (generated results: $\ln(\mathrm{FL}) = 1.51 + 0.307 \star \ln(\mathrm{OTL})$, R-square $= 0.255$ $S_{y \cdot x} = 0.0371$ $y = 3.39$; mean fork length = 29.74 mm, mean otolith total length = 459 μm). The slight overestimate of the true mean fork-length is due to the added size classes at the upper end of the otolith length distribution.

Fork length was plotted against otolith total length from the first 400 random obtained pairs of data, along with frequency distributions of the same statistics from all 10 000 pairs (Fig. 1). From the simulated data, a random sample was taken consisting of 27.2% of the individuals below (small fry) and 43.4% above (large fry) the mean fork length at emergence. This corresponds to the otolith-backcalculated fry to smolt survival pattern in West and Larkin (1987). The pooled population of the two random samples of surviving fry (small plus large fry) showed a shift in mean fork length from 29.72 to 29.97 mm; mean otolith length only shifted from 458 to 461 μm, far from the observed value of 493.6 μm. The simulated shift in mean otolith length, though, is expected to underestimate the true value due to the low correlation between fork length and otolith length. To compensate for this effect, a higher selective mortality was introduced in a new run. A survival pattern was applied to fork lengths that was approximately equal to the one observed for otolith lengths; i.e. a random sample was taken consisting of 10% individuals below and 64% above the mean fork length at emergence. The resultant effects on otolith and fork length distributions are indicated in Fig. 1 as shaded areas and filled squares, respectively. Mean fork length shifted from 29.74 to 30.42 mm as an effect of selection, and mean otolith length only shifted from 459 to 467 μm, still an obvious discrepancy from the mean of 493.6 μm in the surviving smolts in Babine Lake as determined by West and Larkin (1987).

An argument against these results may be that an even greater difference in survival between large and small individuals at emergence could have caused the observed shift in otolith size distribution. To get an idea of a possible survival pattern that would bring about a translocation of mean otolith length from 458 to 494 μm, a series of simulations were conducted. All individuals below an increasing level of length suffered total mortality and all above the same length survived. Thirty-two random trials, each based on 10 000 data-pairs, were conducted as four runs on each of eight fork-length levels: 30, 30.5, 31, 31.5, 32, 32.5, 33, and 33.5 mm. When this mortality pattern was applied to each generated fork-length frequency distribution, an increasing mean fork length of survivors was determined with a corresponding increase in mean otolith length. However, total survival also decreased due to the declining slope on the right-hand side of the length frequency distribution.

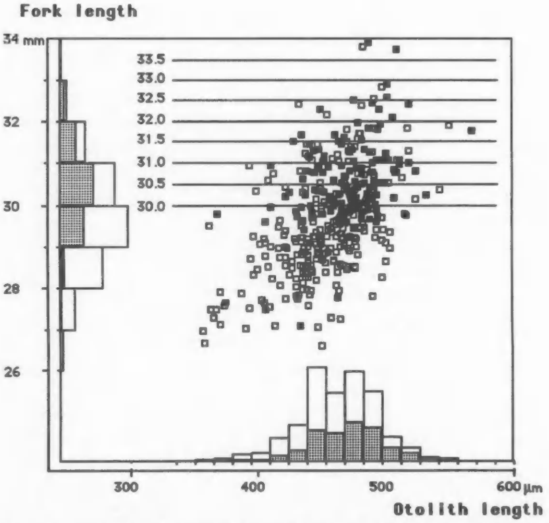

FIG. 1. Simulated data of fork length and corresponding otolith total length based on the pooled population of sockeye salmon at emergence (West and Larkin 1987). The data were obtained using the regression equation of ln fork length versus ln otolith length plus a random normal error with a SD equal to $S_{y \cdot x}$ (0.03717). The first 400 random produced data pairs are plotted in connection with frequency distributions of the same two parameters. Filled squares and shaded areas show the effect of selection on fork length equal to the observed effect on otolith length (mortalities of 90 and 36% below and above mean fork length, respectively). Horizontal lines in the plot designate eight increasing fork length levels for selection (mortalities of 100 and 0%, below and above lines, respectively), the effects of which are shown in Fig. 2.

When survival percentage was plotted against otolith length, a decreasing exponential relationship was found (Fig. 2). From this relationship survival corresponding to a mean otolith length of 494 μm was only 1.42% ($S_{y \cdot x} = 0.28\%$), more than a magnitude lower than the estimated survival in the lake (West and Larkinn 1987). A rough estimate of the 95% confidence limits are 1.42% $\overset{\times}{\div}$ 1.6. (Obtained from regression analysis of ln(survival) versus otolith mean lengths on eight points around 494 μm in the conducted trials).

The randomly generated points in Fig. 2 convincingly demonstrate that the survival corresponding to an otolith length of 494 μm would be significantly less than the lowest stated sur-

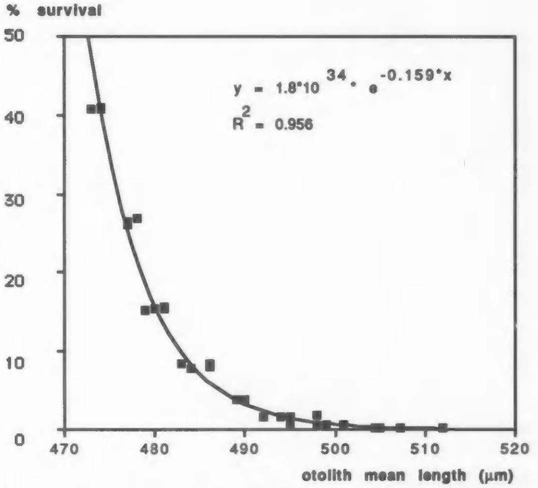

FIG. 2. Population survival percentage and corresponding otolith mean length as a result of a simulated survival pattern of 0% below and 100% above selected limiting fork-length levels. Four independent runs by eight fork-length levels (32 × 10 000 random generated data pairs of fork length versus otolith length) were the basis for constructing the plot. The eight levels of increasing fork length are shown as horizontal lines in Fig. 1. Curve depicts predicted regression-line of ln(survival) versus otolith mean length.

vival of 12.7% in West and Larkin (1987). Furthermore this result was obtained with a very clear division in survival rate between large and small individuals, a survival pattern unlikely to be found in nature. This indicates that an even lower true survival would be necessary to bring about the observed change in the otolith size distribution.

These recalculations show that it was highly improbable that size-selection against small fry at emergence could solely account for the observed shift in the otolith length distribution. The existence of size-selection in the population was by no means ruled out by the results of the current analysis, and a comparison between backcalculated and estimated size distributions from July, when correlation between otolith and fish size was higher, would probably give a better clue to the existence of such a mechanism.

The shift in otolith mean size was, however, so conspicuous that other explanations must be sought. West and Larkin (1987) suggested that otolith length may be better correlated with fry weight than with length. In a study on the relationship between otolith growth and size and development of migratory *Salmo trutta* alevins, otolith size was not better explained by wet weight than by alevin length (H. Mosegaard, unpubl. data). In another study, alevin dry weight at emergence was analysed in relation to different measures of otolith size. Regression analyses resulted in R-square values no greater than 0.20, even though later survival in artificial stream sections showed a clear case of selection for trout with large otolith size at emergence (R. G. Titus, Institute of Limnology, Box 557, S-75122 Uppsala, Sweden, unpubl. data).

It appears that otolith size at emergence reflects determinant properties of an individual fry besides jsut length and weight. Recent investigations have elucidated the low variability of otolith growth rates in relation to variability of fish growth rate (Secor and Dean 1989; Reznick et al. 1989), a condition which leads to a higher slope in the otolith — fish size relationships in slow growing individuals (relative to fast growing ones of the same age). Uncoupling of otolith and fish growth rates in salmonids (Mosegaard and Titus 1987; Mosegaard et al. 1988) had lead to the formulation of an alternative hypothesis where otolith growth is governed by the overall metabolic level of activity in the fish (Mosegaard 1986; Mosegaard et al. 1988). Somatic growth in yolk sac fry may be regarded as unlimited with regard to nutrition. Otolith size at emergence may therefore solely reflect individual metabolic level. The apparent selection for larger otoliths at emergence may therefore be a reflection of a selection for higher metabolic rate, a rate that under favourable feeding conditions may lead to higher growth rate and survival of the fry at later stages. The claimed size-selective mortality in West and Larkin (1987) may therefore be based upon a coincidental association between fish and otolith size at emergence.

The results of the present reevaluation of the data from West and Larkin (1987) also point out some of the difficulties in connection with the common regression-analysis approach inferring life history events at the size-distribution level. If regression equations are used to reconstruct size distributions, serious errors can be introduced if the original distributions are skewed and the variability around the regression line is large.

The relationship between fish size and otolith size at emergence exhibits great variability. Some of this variation may be due to differences in developmental stage and/or in temperature-induced growth rates among fry (Neilson et al. 1985; Mosegaard and Titus 1987). Including both age and temperature into the backcalculation analyses may improve predictability as well as reduce the risk of bias.

At later life stages, differences in the otolith–fish size relationship among fishes with differing somatic growth rates (Reznick et al. 1989; Secor and Dean 1989) will introduce bias into the backcalculation analyses if simple linear equations are assumed, and even greater bias will result if size-selective mortality exists. Development of more tenable procedures of backcalculation and subsequent evaluation of results may be a way to avoid future confusion. One way may be to add several more regressors to the backcalculation, such as age, cumulated otolith size, and temperature, or use randomization modelling to reconstruct the otolith size–fish size development of the population.

I thank Robert G. Titus for valuable discussions, and gratefully acknowledge the financial support from the National Swedish Board of Fisheries Research Council. — H. Mosegaard, *Institute of Limnology, Box 557, S-751 22 Uppsala, Sweden* (J9967)

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Reply to H. Mosegaard on "What is Reflected by Otolith Size at Emergence?"

We have reviewed the comment by Mosegaard (1989) on our paper "Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia" (West and Larkin 1987) and do not disagree with the author. We estimated a selective mortality based on emergent fry length back-calculated from otolith size. Mosegaard suggests selection is related to growth rate and hence to metabolic rate, to which emergent otolith size is closely related and a better indicator. Our own data show a conspicuous shift in otolith size and that the correlation between fork length and otolith size is low ($r^2 = 0.2$) which supports Mosegaard's assessment.

Our use of fork length was a conventional approach, since the concept of size related mortality is well documented for juvenile salmon, for example for pink salmon *O. gorbuscha* (Parker 1971); coho *O. kisutch* (Bilton et al. 1982); and chum (Healey 1982). Neilsen and Geen (1986) did not find conclusive evidence of size selective ocean mortality for chinook salmon (*O. tshawytscha*) but stated that their findings were "consistent with the view that smaller fish were removed from the population at a greater rate." Regarding sockeye fry in Babine Lake, our estimate of linear change in instantaneous mortality rate is consistent with the findings of McDonald and Hume (1984). Their observed differences in survival rates of various marked groups were not significant and differences in mean fork length were small, but as Ricker (1969) points out "a rather large selective mortality is required to produce a rather small shift in mean length."

However, the conventional analysis of size selective mortality should not prejudice the consideration of other characteristics on which selective mortality may act. For instance, Swain and Lindsey (1984) attributed selective mortality of three-spine stickleback to vertebral count without respect to body size. Swain (1988) found selective mortality of peamouth chub to be related to vertebral counts but only over a narrow range of body lengths. Many morphological or physiological factors may be considered, and metabolic rate is certainly a factor of far reaching significance.

The intent of this response, then, is to compliment Mosegaard on his detailed analysis. Our data appear to support his thesis. We would caution, however, against discarding the extensive evidence for size-selective mortality, which may be a reflection of an interdependence of body size, growth rate, and metabolic rate. — C. J. West, *Department of Fisheries and Oceans, 555 W. Hastings St., Vancouver, B.C. V7V 1N6* and P. A. Larkin, *Resource Ecology, University of British Columbia, 2204 Main Mall, Vancouver, B.C. V6T 1W5.*

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Comment on Boisclair and Leggett: Can Eating Really Stunt Your Growth?

Boisclair and Leggett (1989) found a lack of correlation between field estimates of food consumption and relative growth rates of ages 2 and 3 yellow perch (*Perca flavescens*) across 10 lake populations. From these results they imply that food consumption rate estimates for fish populations may not soundly indicate conditions for growth, because of presently inadequate knowledge of fish metabolic cost dynamics. Extensive reference was made to Hayward and Margraf (1987) in which we used field estimates of yellow perch feeding rates as evidence that their growth conditions have been degraded in Lake Erie's western basin.

Boisclair and Leggett suggest that three factors detract from the strength of our conclusions. They state that our study was "limited by the number of situations studied ($n = 2$)." We are concerned that this suggests that we sampled at only two sites when, in fact, we reported results for four stations in 1983, two each in the western and central basins.

They further suggest that our findings of higher yellow perch feeding rates in the central versus western basin may be inaccurate because we used instantaneous stomach evacuation rates (R) that were derived from Persson's (1979) model, which considers only water temperature and not prey type as the influencing variable. Persson's (1979) study demonstrated that R values in perch did not differ significantly over an array of invertebrate diet taxa which were similar to those most frequently consumed by perch in our study. He did find that food was evacuated at a lower rate for a given temperature, when perch were given a diet of fish (Persson 1981). To conservatively check our findings, I used the lower value of *R* and recomputed food consumption estimates for the large size-group of yellow perch (140–195 mm TL) at the Fairport station (central basin) although fish represented only negligible portions of the diets. Higher feeding rates for central basin fish in the large size-group was our most critical result, and a lower value of *R* will give a lower estimate of daily rations. Even with this conservative measure, food consumption rates for yellow perch at Fairport exceeded maintenance rations by factors of 2.9, 3.4, and 1.4, versus only 1.6, 2.0, and 1.2, at the Middle Sister site (western basin) for spring, summer, and fall diel collections, respectively.

Their most important criticism was that our apparent yellow perch growth data from 1983 "do not support (our) interpretation of between-basin growth differences." In this way, they imply that growth rates of western and central basin yellow perch in 1983 are incongruent with our estimates of food consumption rates in each basin. We hypothesized that conditions for yellow perch growth had declined in Lake Erie's western basin based on long-term trends in population survey data (figure 1 in our paper), and declines in mean yellow perch sizes in western basin commercial fishery catches. We indicated that apparent growth rates of ages 2 and 3 yellow perch from our 1983 collections (figure 9 in our paper) were most negatively biased by heavy commercial fishing pressure in the central basin in October. Because apparent growth rates were known to have been biased by effects of the size-selective fishery, we did not extensively analyze agreement between apparent growth patterns and food consumption estimates. We did note that a flattening out of apparent growth patterns of age 3 yellow perch after July at western basin sites, corresponded with directly estimated declines in feeding rates.

Despite our mention of negative bias, Boisclair and Leggett computed absolute growth rates (AGRs) for yellow perch at the Middle Sister (western basin) and Fairport (central basin) stations from our 1983 apparent growth (in wet weight) data. Moreover, they used only the first and end-of-year mean weight values for each age-class (estimated from our figure 9). They then computed relative growth rates (RGRs) by dividing AGR by some estimate of mean weight for the entire sampling period. Their approach, therefore, ignored the many temporally intermediate estimates of yellow perch mean weight and, by focusing on only the beginning and ending mean weight values, emphasized the fishery-related negative bias in apparent growth in the central basin.

They concluded that age 3 yellow perch did indeed grow much faster on both an absolute and relative basis in the central versus in the western basin. They found, however, that only AGRs of ages 1 and 2 yellow perch were greater in the central basin while RGRs were higher for these younger fish in the western basin. Higher RGRs would be expected for similar-sized fish feeding at higher weight-specific rates.

To clarify this, I have computed age-specific, AGRs and RGRs for yellow perch at the Middle Sister and Fairport sites from the apparent growth data (as in our figure 9). AGRs were determined by fitting all mean wet weight data from the western basin site, and all but the end-of-year data (all data were used for age 1 fish) from the central basin site, to linear models. AGRs were taken as the slopes of the resultant linear models which were generally well-fit by the apparent growth data. These were then converted to RGRs by dividing by mean weight for the sampling period, as Boisclair and Leggett did. The only major difference in my approach was that end-of-year weight declines for ages 2 and 3 central basin fish, which we confidently attributed to fishery effects, were deemphasized.

Results of my analysis showed higher AGRs for ages 1–3 yellow perch in the central basin as we stated in our paper (values of 0.08, 0.12, 0.08, and 0.15, 0.26, and 0.88, for ages 1–3 fish in the western and central basins, respectively). AGR was not an increasing function of fish size in the western basin (as they suggested) due to the severely depressed AGR of age 3 yellow perch. My analysis showed higher RGRs for ages 2 and 3 fish in the central basin (values of 0.007, 0.004, 0.002, and 0.006, 0.005, and 0.008, for ages 1–3 fish in the western and central basins, respectively).

I do concede that a slightly higher RGR was indicated for age 1 yellow perch in the western (0.007) versus central (0.006) basin. Reexamination of our results, however, shows that this is not incongruous with our food consumption rate data. We showed that feeding rates (beyond maintenance rations) were marginally greater in the central basin for yellow perch in the small size-group (composed of age 1 and 2 fish in the western basin but only age 1 fish in the central basin). Food consumption rate was shown to be an inverse function of yellow perch size in the western basin (see our figure 8, where age 1 yellow perch fell largely within the 75–100 mm TL length-group). Hence, feeding rates of age 1 western basin yellow perch alone, were higher than those indicated for the small size-group which included both ages 1 and 2 fish (see our figure 6).

Our primary argument was that the greatest interbasin disparity in conditions for yellow perch growth, as indicated by very pronounced differences in food consumption rates, existed for fish in the 140–195 mm TL size-group. This included only age 3 fish in the western basin (RGR of 0.002), and ages 2 and 3 fish in central basin (RGR of 0.005 and 0.008, respectively). Hence, even their crude analysis of our apparent growth data supports our main contention. We recognize, in retrospect, that it is not readily apparent to readers that different age-classes composed the small (85–139 mm TL) and large (140–195 mm TL) size-groups in each basin.

Finally, Boisclair and Leggett (1989) imply that we did not express food consumption rates on a relative (predator-weight-specific) basis, stating that we "did not provide the data required to estimate RDR (relative daily ration) for these fish." All of our food consumption results were, in fact, expressed relative to predator weights.

From their findings, Boisclair and Leggett suggest that commonly observed density-dependent growth relationships for fish populations may not arise from compensatory changes in food quantities consumed by individuals, adding that food consumption estimates have never accompanied such studies. Persson (1986) demonstrated that the reduction of a competing roach (*Rutilus rutilus*) population in a shallow eutrophic lake, resulted in both increased food consumption and growth rates of ages 1–3 perch (*Perca fluviatilis*), contrary to their assertion.

Boisclair and Leggett, by process of elimination, attribute their lack of correlation between yellow perch food consumption and growth rates to activity metabolism, presently one of the least well-understood fish bioenergetics parameters. While I agree that better understanding of activity-related costs in fishes is needed, other factors may explain this lack of correlation that they observed across their study lakes. One equally plausible alternative hypothesis, for example, could be that certain of their yellow perch populations represented genetically distinct ecotypes with varying food conversion efficiencies due to differences in standard metabolic rates. Also, they apparently sampled only limited nearshore areas in each lake and assumed that food consumption levels indicated from these limited areas, reflected the complete energy intake experiences which determined sizes of fish collected there. Coverage of spatial as well as temporal variability is critical in food consumption studies for fish populations. In our study, we showed at least some evidence of spatial similarity in food consumption rates within each basin.

Two other analytical shortcomings may also have contributed to their findings. Their expression of food consumption as a single, temporally integrated value for each lake/age-class combination, ignores the shapes of seasonal feeding patterns associated with each data point. Two feeding patterns may have given the same integrated value (their RDR) but have led to different growth rates if one had higher values during periods when the thermal scope for growth was higher.

Also, by showing similar thermal regimes in each lake, readers may assume that temperature influences on yellow perch bioenergetic parameters were equivalent across study lakes. Weight-dependence of bioenergetics parameters was less well-controlled, however, with mean weights ranging as much as five-fold across lakes within a given age-class. As an example, their analytical approach assumes that relative growth of a 6.8 and 33.0 g, age 2 fish, would be equal if they consumed the same relative food weights. Condrey's (1982) treatment of Elliot's (1975a,b) experimental data for brown trout (*Salmo trutta*), for example, suggests that this assumption is incorrect and may have introduced error into their correlation analyses. In a related way, it is noteworthy that the two populations with the smallest age 2 fish (lakes 6 and 8) appear to exclusively account for the lack of correlation between food consumption and growth for this age-class. Analyses based on more restricted size-classes, rather than by age-classes, may have been more appropriate.

Finally, in connection with their comments concerning the yellow perch bioenergetics model of Kitchell et al. (1977) and activity metabolism, we have found (Hayward and Margraf 1988) that reasonable estimates of yellow perch food consumption rates can be attained with this model, even when no activity-related metabolic cost is assumed (active/standard ratio of 1). Using a Western Lake Erie thermal regime and relatively unbiased yellow perch growth data as input, a bioenergetics model-derived seasonal pattern of food consumption rates was strikingly similar to the food consumption pattern that we determined directly, based on the Elliot and Persson (1978) method. This result supports the more widely accepted direct relation between food consumption and growth and indicates a lesser importance of activity-related metabolism than is suggested by Boisclair and Leggett — R. S. Hayward, *School of Forestry, Fisheries and Wildlife, 112 Stephens Hall, University of Missouri, Columbia, Missouri 65211, USA.*

(JA204)

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On the Relationship between Growth and Consumption Rates: Response to Comments by R. S. Hayward (1989)

We recently assessed the influence of a suite of specific biological variables in explaining among-population variability in fish growth rates (Boisclair and Leggett 1989a,b,c). The species chosen for study was the yellow perch *Perca flavescens*. The variables we examined were the quantity of food consumed, prey types comprised in the diet (taxonomic groups and size classes), and the fish community structure (numerical density and biomass of individual or groups of species). We concluded that the quantity of food consumed by fish played a secondary role in explaining among-population variability in fish growth rates (Boisclair and Leggett 1989a). We further compared our results with those of Hayward and Margraf (1987); to our knowledge, the only other comparative study based on field derived values of growth and food consumption rates. Our analysis of their results lead us to conclude, for the three perch age classes examined, it was very difficult to assess whether growth differences between the western and central basins from Lake Erie were related to differences in the quantity of food consumed. In responding to our paper Hayward (1990) has raised two issues, our analysis of his data, and his interpretation of ours. In the response which follows we deal with these two issues separately.

Response to the Comments on our Analysis of Hayward and Margraf (1987)

Sampling sites and stations

We recognized the fact that Hayward and Margraf executed their sampling at many stations in both the western and the central basins of Lake Erie. This, however, does not change the fact that in their paper they principally compared the growth rates of perch from two basins and that for any age or size class the analysis related to comparisons between two areas; the western and the central basin of Lake Erie. Hence, our criticism stands.

Prediction of Perch Gastric Evacuation Rates from Water Temperature

In their study, Hayward and Margraf estimated the quantity of food consumed by perch using gastric digestion rates predicted from water temperature (Persson 1979). This procedure is adequate for perch populations consuming a composite of *Gammarus*, *Chaoborus*, chironomids and zooplanktonic organisms; the prey items used by Persson (1979) to construct the relationship between perch gastric evacuation rate and water temperature. We question its validity, however, when, as is the case in Lake Erie, hard to digest food items such as *Sphaeriidae* comprise a large fraction of fish diet. *Sphaeriidae* occurred in approximately 20 to 50% of the perch stomach they examined (both basins) during the summer and more than 50% in the fall (western basin only). The occurrence of *Sphaeriidae* in the diets varied greatly among perch size classes and between basins, but appears to have increased sharply with perch size. While knowledge of the percent contribution of *Sphaeriidae* to perch diet would be more useful than percent occurrence in assessing the potential influence of *Sphaeriidae* on gastric evacuation rates, the level of occurrence reported by Hayward and Margraf suggests that their predicted gastric evacuation rates may have departed substantially from those actually experienced by the fish they studied. It is important to note that the bias induced by the presence of *Sphaeriidae* in the diet could either increase or decrease between-basin differences in food consumption rates depending on how percent occurrence translates to percent contribution to perch diet in both basins.

Between-Basin Differences in Growth Rates

Our analysis of the Hayward and Margraf data, executed on a relative (RGR: g wet$\cdot$ g wet$^{-1}\cdot$d^{-1}) rather than an absolute basis (AGR: g wet$\cdot$ d^{-1}), suggested that, contrarily to their interpretation, perch aged I+ and II+ grew faster in the western than in the central basin of Lake Erie (Boisclair and Leggett 1989a). In this case, the relationship, if any, between growth and food consumption would have a negative slope.

From our perspective, the more precise results provided by Hayward (1990) show that, given the error around their estimates, age I+ and II+ perch from the central and western basins grow at similar rates (age I+: RGR = 0.007 in western and 0.006 in central basin; age II+ RGR = 0.004 in western and 0.005 in central basin). Interestingly, this situation in which growth rates do not appear to vary but in which there are potential food consumption rates differences (depending on the outcome of the influence of *Sphaeriidae* on gastric evacuation rates and food consumption rates) supports our contention (Boisclair and Leggett 1989a) that the relationship between in situ growth and consumption rates for these age classes is weak. As Hayward (1990) correctly notes the case of age III+ perch is obscured by the presence of size selective sampling particularly for the Fairport station of the central basin. Our calculations of age III+ growth rates, and those of Hayward (1990), coincide for the Middle sister station of the western basin (RGR = 0.002) but vary by two-fold for the Fairport station of the central basin (RGR = 0.004 (Boisclair and Leggett) or 0.008 (Hayward)). The difference between these estimates is largely due to our exclusion of their September value for age III+ perch mean weight at the Fairport station. We excluded the September data because, while their figure 9 suggests that age III+ perch from that station virtually double their weight from July to September (which is rather improbable), none of the other stations from that basin show such an extreme pattern. Despite this difference, however, our calculations agree with those of Hayward; age III+ perch do grow more rapidly in the central than in the western basin.

The completion of our analysis of their data was impeded by the lack of food consumption rates specific to the different perch age classes studied. If we accept the food consumption rates estimated by Hayward and Margraf (1987), it is reasonable to hypothesize that the growth differences observed for age III+ perch between the western and the central basin of Lake Erie may be related to feeding regimes. However, a rigorous evaluation of such a hypothesis requires more than a comparison of two points (central and western basins). The search for general patterns can only be achieved by looking at many different systems. This was the purpose of our own study. It is important to note that, despite a comparative study of 12 perch populations, our work too was confronted with the problem of alternate hypotheses.

Response to the Comments on Boisclair and Leggett (1989a)

Hayward (1990) notes that Boisclair and Leggett (1990) omitted reference to the work of Persson (1986). This was intentional. In this excellent work, the increase in both perch (*Perca fluviatilis*) growth and consumption rates was obtained following the experimental manipulation of the roach *Rutilus rutilus* population (40% reduction in roach population biomass, 70% reduction in roach numerical abundance). The results of this work thus corresponded more closely to the third paper of our series which dealt with the influence of fish community biomass and numerical density on perch growth (Boisclair and Leggett 1989c). Furthermore, we believe that results from a comparative approach (our work and that of Hayward and Margraf (1987)) do not necessarily parallel those of the experimental approach (Persson 1986). For instance, a system recuperating from a strong and punctual disturbance, as was the case in Persson's study, might not have the same properties and dynamic as the populations we studied.

Spatial and temporal sampling schedules are critical to any study as is the scale examined. Like Hayward and Margraf (1987), we sampled many stations in the lakes we studied. However, most of our lakes were probably smaller than their "stations." In our work, we assumed that sampling at different stations within a given lake would not bias the results (i.e. growth and related processes would not vary much across stations). This assumption was supported by the lack of significant differences between perch growth rates in various regions of Lake Memphremagog (pelagic and littoral; northern and southern parts of the lake), the largest lake we sampled (Gascon and Leggett 1977; Boisclair and Leggett 1989a).

In our study, and in that of Hayward and Margraf (1987) perch consumption rates were lower in late May and September than during the months of July and August. This observation, together with the similarity of the water temperature regimes of the lakes we studied, suggest that thermal scope for growth was relatively similar among lakes.

We have had a constant debate between ourselves, our colleagues, and our referees regarding the best way to analyze our data (absolute versus relative rates, and grouping by age or size classes). In his comments, Hayward (1990) continued this debate by suggesting that an analysis using size classes would be more appropriate because of the potential weight-dependence of some bioenergetics parameters (Condrey 1982). It is worth noting that the data set used by Condrey (1982) to analyse the weight-dependence of some bioenergetics parameters covered a 20-fold difference in fish weight (Condrey 1982; Elliott 1975a,b). The mean fish weight for the age classes we studied varied from three- to five-fold among populations. While it is

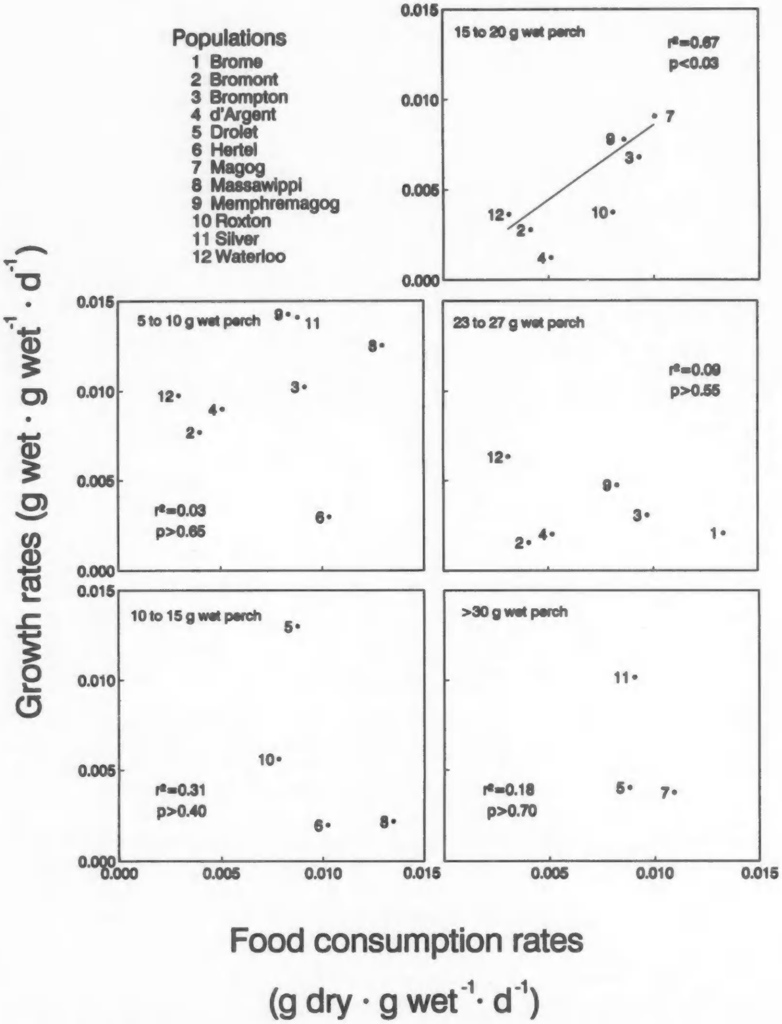

FIG. 1. Relationships between growth rates and consumption rates for five perch size classes.

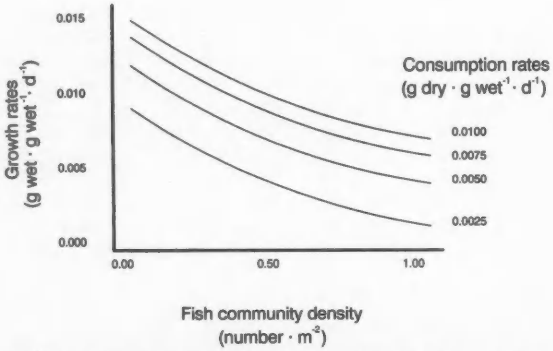

FIG. 2. Multivariate model relating fish growth rates to total fish community numerical density and food consumption rates.

not our purpose to comment on the analysis of Condrey (1982), we argue that in our analyses the influence of weight-dependence invoked by Hayward (1990) is minimal.

When plotted by size classes, our data show a significant relationship between growth rate and food consumption rate only for 15- to 20-g perch. A significant relationship could also be created for 5- to 10-g perch by excluding Lake Hertel from the analysis, although we known of no reason to do so (Fig. 1). For the remaining three other size classes no pattern emerges. Consequently, even when analysed on a size-class basis, our results suggest that variables other than consumption rates strongly influence fish growth.

Subsequent analyses revealed that the numerical density of the total fish community was a key variable in explaining among-population variability in fish growth rates (Boisclair and Leggett 1989c). Further, we hypothesized that this variable may represent an integrated measure of activity and/or density-dependent stress related costs. On a multivariate basis, the strongest and most consistent model explaining among-population variability in fish growth rates combined the influence of fish community numerical density and food consumption rates (Fig. 2). Fish community numerical density ($\text{number}\cdot\text{m}^{-2}$) explained an average of 60% of the among-population variability in fish growth rates while food consumption rates explained approximately 30% (Boisclair and Leggett 1989c). This relationship suggests that, at equivalent fish numerical densities, the quantity of food consumed may have an important influence on fish growth. Moreover, the influence of fish community density may explain why the Kitchell et al. (1977) model, which is based on the relationship between fish growth and feeding level, often fails to adequately predict food consumption rates (Boisclair and Leggett 1989d). Taken together, our work (Boisclair and Leggett 1989a,b,c,d) should be perceived, not as a rejection of the relationship between fish growth and consumption rates, but as an important reminder that other factors, some of which are potentially more important than consumption rates, can strongly interfere with this intuitively pleasing relationship.

Acknowledgements

We thank Dr. R. S. Hayward for showing interest into our work, for providing a more detailed analysis of his study, and for giving us the opportunity to present additional details on some aspects of our own work — D. Boisclair and W. C. Leggett, *Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, Que. H3A 1B1 Canada.*

(JA318)

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ANNOUNCEMENT/AVIS

Aquatic Toxicity Workshop

The 17th Annual Aquatic Toxicity Workshop will be held at the Hotel Vancouver, Vancouver, British Columbia, on November 5–7, 1990. The theme of the Workshop will be Threshold Biological Responses: Predicting and Determining Ecological Relevance. Major topics will include (i) methodology and development: the tools and the practice, (ii) histopathological responses: so what if fish have lesions, (iii) genotoxic/cytotoxic responses, (iv) acute versus chronic responses, (v) exotic chemicals: managers, scientists and the public, (vi) toxicology and sustainable development, and (vii) toxicological and industrial regulation: new approaches and procedures. A plenary session will be held on Predicting and Monitoring Biological Effects. Focus of the Workshop will be on major water bodies of concern including the Fraser River, the St. Lawrence, Halifax Harbor, Vancouver Harbor, and Puget Sound. Platform and poster presentations will be accepted in English or French, and submissions must be received by August 31, 1990 to be considered. For further information, please contact Dr. Peter M. Chapman, Program Chair, c/o E.V.S. Consultants, 195 Pemberton Avenue, North Vancouver, British Columbia, V7P 2R4 Canada. Telephone (604) 986–4331. FAX (604) 662–8548.

Atelier annuel sur la toxicité aquatique

Le 17e Atelier annuel sur la toxicité aquatique se tiendra du 5 au 7 novembre 1990 à l'hotel Vancouver, à Vancouver (Colombie-Britannique). L'atelier aura pour thème: Les réponses biologiques seuils: prévision et détermination de la pertinence écologique. Les principaux sujets traités seront: i) La méthodologie et le développement: les outils et la pratique; ii) Les réponses histopathologiques: les lésions des poissons; iii) Les réponses à la génotoxicité et à la cytotoxicité; iv) Les réponses aiguës ou chroniques; v) Les produits chimiques spéciaux: les gestionnaires, les scientifiques et le public; vi) La toxicologie et le développement soutenu et vii) Toxicologie, industrie et réglementation: approches et procédures nouvelles. Il y aura une séance plénière qui portera sur la prévision et le contrôle des effets biologiques. Les travaux de l'atelier seront surtout axés sur les principaux plans d'eau sources d'inquiétudes, notamment les fleuves Fraser et Saint-Laurent, les ports d'Halifax et de Vancouver et le détroit Puget. Les présentations, sous forme d'exposés ou d'affiches, peuvent être soumises en Anglais ou en Français et doivent être reçues au plus tard le 31 août 1990. Des renseignements supplémentaires peuvent être obtenus auprès du Dr. Peter M. Chapman, responsable du programme, a/s E.V.S. Consultants, 195 avenue Pemberton, North Vancouver, Colombie-Britannique, V7P 2R4. Tél.: (604) 986–4331, FAX: (604) 662–8548.

Guide for Authors

Introduction

We welcome manuscripts reporting significant new information in fisheries and aquatic sciences. Manuscripts may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and cover numerous disciplines including biology and ecology of marine and freshwater organisms, physiology, toxicology, genetics, limnology, oceanography, economics, disease, and management.

Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented. Preference will be given to those whose experimental results emphasize causal mechanisms underlying observed phenomena rather than pure description and fact. Manuscripts should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. Their novelty must relate to more than the particular (a certain year, place, taxon, chemical compound) and their contribution to science must clearly be beyond the confirmatory state.

Manuscripts submitted should be as comprehensive as possible; research fragments are generally unacceptable. If a single paper cannot be produced, then closely related papers should be cross-referenced and submitted together. The paper should not be submitted or accepted for publication elsewhere.

The *Journal* considers the following types of contributions:

Articles: Studies of broad scope that are original contributions to science.

Reviews: Detailed critical appraisals of broad areas of investigation, particularly those that have developed rapidly in recent years.

Perspectives: Essays of opinion or hypothesis on aquatic science of concern to the professional and layman. References are desirable; informal style is welcome.

Comments: Opinion on topics recently discussed in the *Journal*; preferred maximum length, 500 words.

Manuscript Submission

Submit manuscripts in triplicate to the Editor, accompanied by a covering letter that (1) states the main points and significance of the work, (2) accepts the mandatory $44 page charge, (3) suggests potential referees, and (4) identifies other manuscripts containing the same or similar information. Original typescripts and figures (except halftones) are best retained by the author until requested.

Each manuscript is normally submitted to two referees for appraisal before final evaluation by an editor. However, the Editor will return unreviewed those manuscripts that do not fall within the *Journal's* editorial policy or scope.

Editorial Practices

The *Council of Biology Editors Style Manual* (5th ed. CBE, 9650 Rockville Pike, Bethesda, MD 20814) is used as the authority in matters of form. The standards for spelling are either *Webster's Third International Dictionary* or the *Oxford English Dictionary* and *Le Grand Larousse encyclopédique*. Authors are responsible for consistency in spelling. Titles of periodicals are abbreviated as in *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103). Authors are responsible for ensuring the accuracy and completeness of their reference list. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (4th ed. 1980). Spec. Publ. No. 12, American Fisheries Society. All measurements must be metric, use SI symbols in most instances (exceptions noted in editorial in the *Journal*, Vol. 40, No. 12), and adhere to the *Canadian Metric Practice Guide* (CAN3-Z234.1-79 (Canadian Standards Association, 178 Rexdale Boulevard, Rexdale, Ont. M9W 1R3).

Series titles should be avoided. An abstract is required for all manuscripts and should state concisely, in up to 175 words, what was done, found, and concluded.

Proofs are sent to the author, who is responsible for correcting errors in typesetting. *Alterations to the content must be avoided.*

Fifty reprints are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent with the proofs).

Preparation of Manuscripts

General Guidelines

Movement of manuscripts through review channels and the editorial office is greatly expedited if manuscripts are prepared in *Journal* style and format. When in doubt about specific details, consult a current issue of the *Journal*. General guidelines follow.

Type the manuscript on white paper, preferably 21.5 × 28 cm (8.5 × 11 in.), on only one side of the page. Leave all margins at least 2.5 cm wide.

Type only the title, authors' names and affiliations, and related footnotes on the first page. Number all pages beginning with the title page, including those for tables and captions for illustrations.

Double-space all parts of the manuscript, including tables, captions for tables and figures, footnotes, and the reference list. Underline only material that is to be printed in italics.

Do not use all capitals anywhere in the manuscript.

Use the name-and-year system for literature citations.

Checklist for Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately in a data or manuscript report or at a data repository?

If statistical analysis is included, is it subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report? Does the *abstract* give the essentials of the new knowledge? Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of *materials and methods* limited to what scientists need to understand the design of the study and to judge the adequacy of the data? Are generalizations from the *results* supported by the data provided? Are findings distinguished from inferences? Is the *discussion* limited to interpretation and significance of the findings?

The most common technical problems in submitted manuscripts are listed below. Authors can hasten the processing of their papers if they pay attention to these points during manuscript preparation.

1) Insert bibliographic strip before the abstract (Authors, date, title, Can. J. Fish. Aquat. Sci.).

2) Limit abstract to one paragraph of about 175 words.

3) Double-space all elements of the manuscript, including references, table captions, and figure legends.

4) Avoid exclusive use of capitals everywhere in the manuscript, including headings, table captions, and figure legends.

5) Underline only Latin names of organisms and certain statistical and mathematical notation to indicate italics.

6) Use correct SI symbols for units or measure in figures, tables, and text. Place a zero before the decimal for numbers less than unity.

7) Avoid ambiguous forms such as g $\mathrm{C/m^2/d}$; use g $\mathrm{C{\cdot}m^{-2}{\cdot}d^{-1}}$.

8) Identity test used to test statistical significance and give probability value. No reference is needed for common statistical tests.

9) In the text, generalize from tables and figures; avoid repeating all the details. Be sure each table and figure can stand on its own and is referred to in the text in numerical order. The captions should explain the purpose of the table or figure.

10) Include acknowledgments section at manuscript stage, not when galley proofs arrive.

11) Provide the person's initials and mailing address when referring to personal communications.

12) Delete unnecessary references that do not apply directly to the problem.

13) Check references carefully against test citations and vice versa to ensure exact correspondence. Provide an availability statement for less easily retrieved material, e.g. available from Department of Economics, Simon Fraser University, Burnaby, B.C. V5A 1S6.

14) Delete commas between name and date in citations such as (Smith 1900) and do not underline "et al."

15) Replace 10^n in table headings and figure axes with appropriate SI prefixes or use words (e.g. thousands).

16) Photocopies of figures, except halftones, are appropriate for review purposes. Send photographic prints of figures, or originals if they do not exceed 21.5 × 28 cm, on request for publication. Use the same type of lettering throughout if possible.

Parts of the Manuscript

Organization

Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in presentation of manuscripts.

See that everything in each section is relevant to the heading, and everything in each paragraph to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

Title

Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (1) it allows the reader to judge whether or not the article is of potential interest and (2) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximum amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g. X ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to . . ." or "Investigations on . . ." Good titles greatly assist scientists and librarians in using scientific literature and aid indexers preparing titles for keyword indexes.

Abstract

The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as ". . . is discussed" or ". . . was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents.

Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

Materials and Methods

Materials and Methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine . . . we . . ." If the section is long, consider using subheadings corresponding to headings for the findings.

Results

Limit the results to answers to the questions posed in the purpose of the work, and digest them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made and so avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the test what is clear from the titles. Material supplementary to the text can be archived in the report literature or a recognized data depository and referenced in the text.

Discussion

Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

Acknowledgments

We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence. Nearly every manuscript submitted to the *Journal* contains errors in the references.

Tables

Tables are used to present repetitive data and should be as economical of space as possible.

Design tables to fit a 1-, 1½- or 2- column width of the *Journal*.

Type each on a separate page and number with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Table captions should be succinct and identify the purpose of the table sufficiently well to allow the table to stand on its own.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines.

Figures

Provide photographic reproductions or the original artwork (no larger than 21.5 × 28 cm) of each illustration. If submitting photographs, type the author's name and figure name on a strip of paper and fasten to the back of the print. Do not write on the illustration itself. Provide two photocopies of line illustrations and two sets of any photographs for review purposes.

Design figures to fit a 1-, 1½-, or 2-column width of the *Journal* and ensure that all lettering, numerals, and symbols are legible, neat, and at least 1.5 mm high when reduced. Figures should not be mounted, stapled, or clipped. When possible, figures should be grouped and be done with the same or similar type of lettering.

Type legends in succession on a separate page. Add bar scales to maps, photomicrographs, equipment diagrams, etc.

Where each figure is first referred to, type "Fig. — near here."

Computer-generated figures should be avoided if possible, as they usually reproduce poorly. Dot-matrix printers cannot produce sufficiently dark, solid lines to ensure legibility. Figures drafted in black india ink are always preferable. If sheets of printed characters are used, be sure they adhere completely.

Draft rather than type axis labels for graphs.

Color plates are very expensive to produce and should only be used where the color being presented is essential to the understanding of the text. Extra costs for the reproduction of color plates are usually charged to the author. Submit only the most outstanding photographs for color reproduction. We prefer to use color photographs, but will accept drawings, color negatives, slides, or film positives.

Mathematical Expressions, Equations, and Formulae

Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulae. In the various expressions, place each component in its correct position.

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the number *one*, and between the capital *O*. and the numeral *zero*. Make other explanatory notes similarly.

Appendix

Abbreviations

Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

becquerel	Bq
calorie	cal
centimetre	cm
centimetre, square	cm^2
centimetre, cubic	cm^3
centimetre per gram per second	$cm \cdot g^{-1} \cdot s^{-1}$
coulomb	C
day	d
decimetre	dm
degree Celsius	°C
degrees of freedom	df
gram	g
hectare	ha
hertz	Hz
hour	h
joule	J
kilometre	km
litre	L
lumen	lm
lux	lx
metre	m
metre, square	m^2
metre, cubic	m^3
micrometre	µm
milligram	mg
millilitre	mL
millimetre	mm
millimetre, square	mm^2
minute	min
molar mass	M
mole	mol
mole per litre	mol/L, M
month	mo
Pascal	Pa
second	s
standard deviation	SD
standard error	SE
tonne	t
volt	V
volume	vol
watt	W
week	wk
year	yr

Dates

Dates may be written in the sequence day-month-year without internal punctuation (On 9 October 1983 the . . .), or the alternative sequence month-day-year may be employed with the year set off by commas before and after it (On October 9, 1983, the . . .).

Reference Citations in Text

Name-and-year system

The *Journal* uses the name-and-year system of citation; that is, the surname of the author(s) and the year of publication are inserted in the text at an appropriate point: "Brown (1983) compared . . ." or ". . . were compared (Brown 1983)." If the reference has more than two authors, include only the surname of the first author followed by "et al." (not italicized): "Brown et al. (1983) compared . . ." or ". . . were compared (Brown et al. 1983)."

Personal communications

Personal communications are not listed in the reference list. Using parentheses in the text, state the name and mailing address of the communicator followed by "pers. commun."

Unpublished data

If the unpublished book or article has been accepted for publication, list it in the reference list section followed by the notation "(In press)." Only those manuscripts that are in galley or page proof or for which there is an acceptance letter can be considered in press. If the article is submitted but not yet accepted, state the name and address of the author of the unpublished material followed by the notation "unpubl. data" in the text and do not include it in the reference list.

Reference Lists

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *Serial Sources for the BIOSIS Data Base*) for references.

Journal article

PETERMAN, R. M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. 39: 1444–1452.

Entire issue of journal

GORDON, D. C. JR., AND A. S. HOURSTON [ED.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40(Suppl. 1): 1–365.

Book in a series

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Book not in a series

LEBLOND, P. H., AND L. A. MYSAK. 1978. Waves in the ocean. Elsevier, New York, NY. 602 p.

Part of book

HEALEY, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. p. 203–229. *In* W. J. Neil and D. C. Himsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, OR.

Corporate author

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, DC. 1193 p.

Theses

Kutty, M. N. 1966. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, Univ. Toronto, Toronto, Ont. 102 p. Natl. Libr. Can., Can. Theses Microfilm No. 646.

Reports

Smith, J. E. 1981. Catch and effort statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1032: 90 p.

Translation

Koike, A., and M. Ogura. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64: 1–11. (Transl. from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983)

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h," "min," and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Word List

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the *Journal's* house style for these commonly used terms:

age-class (n.)
age-group (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
short term (n.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t-test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

Guide des auteurs

Introduction

Les manuscrits comportant une information nouvelle dans le domaine des sciences halieutiques et aquatiques sont les bienvenus. Ils peuvent se rapporter aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influencent les systèmes de production aquatiques, et couvrir de nombreuses disciplines, y compris biologie et écologie des organismes marins et dulçaquicoles, physiologie, toxicologie, génétique, limnologie, océanographie, économique, maladies et gestion.

Les critères de sélection des manuscrits dépendent de l'étendue et de l'importance des connaissances ou idées nouvelles qu'ils contiennent. On donnera la préférence à ceux dont les résultats expérimentaux font ressortir les mécanismes sousjacents aux phénomènes observés plutôt qu'une simple description ou énoncé de fait. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles en faisant plus que corroborer des faits.

Les manuscrits soumis devraient être aussi complets que possible; des fragments de recherche sont généralement inacceptables. S'il est impossible de produire un seul article, on devra soumettre ensemble des articles étroitement liés entre eux, avec références croisées. L'article ne doit pas avoir été soumis ou accepté pour publication ailleurs.

Le *Journal* considère les types de contributions suivants :

Articles : études d'une portée générale, constituant des contributions inédites à la science.

Critiques : appréciations critiques détaillées de vastes champs de recherche, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives : essais portant sur une opinion ou une hypothèse relative aux sciences aquatiques qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans une style simple.

Commentaires : opinions sur des sujets récemment exposés dans le *Journal*, et, de préférence, ne dépassant pas 500 mots.

Soumission des manuscrits

Les manuscrits doivent être soumis au rédacteur en triplicata, et accompagnés d'une lettre mentionnant : 1) les principaux points et l'importance du travail, 2) l'acceptation des frais de publication obligatoires de 44 $ par page, 3) des suggestions quant aux arbitres éventuels et 4) une mention d'autres manuscrits contenant une information identique ou qui se rapproche de celle contenue dans le manuscrit soumis. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les simili) jusqu'à ce qu'on les lui demande.

Un manuscrit est normalement soumis à deux arbitres pour évaluation, avant l'évaluation finale par un rédacteur. Cependant, les manuscrits qui ne répondent pas à la politique éditoriale ou à la portée du *Journal* sont retournés à l'auteur sans avoir été soumis à l'arbitrage.

Dispositions générales

Le *Council of Biology Editors Style Manual* (5^e éd., CBE, 9650 Rockville Pike, Bethesda, MD 20814) sert de guide quant à la forme de la présentation. Le *Webster's Third International Dictionary* ou l'*Oxford English Dictionary*, et le *Grand Larousse encyclopédique* font autorité pour l'orthographe des mots. L'uniformité de cette dernière est la responsabilité des auteurs. Les titres de périodiques sont abrégés suivant les *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103). C'est la responsabilité des auteurs de s'assurer que leurs références sont complètes et exactes. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (4^e éd. 1980), Spec. Publ. No. 12, American Fisheries Society. Toutes les mesures doivent être conformes au système métrique et, dans la plupart des cas, être exprimées en unités SI (sauf exceptions mentionnées dans un éditorial du *Journal*, vol. 40, n° 12), et se conformer au *Guide canadien de familiarisation au système métrique* CAN3-Z234.1-79 (l'Association canadienne de normalisation, 178, boul. Rexdale, Rexdale (Ont.) M9W 1R3).

On devra éviter les titres en séries. Un résumé doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé.

L'auteur doit revoir les épreuves qu'on lui remet et en corriger les erreurs typographiques. *Il doit éviter de modifier le contenu du texte.*

Cinquante tirés à part sont fournis gratuitement. Des tirés à part supplémentaires peuvent être achetés au moment de la publication (un bon de commande à cet affet accompagne les épreuves).

Préparation des manuscrits

Directives générales

La marche des manuscrits à travers les diverses étapes de l'arbitrage et de la révision sera grandement facilitée si les articles sont préparés dans le style et le format du *Journal*. En cas de doute sur des points particuliers, veuillez consulter une livraison récente du *Journal*. On trouvera ci-dessous des directives générales.

Dactylographiez le manuscrit sur papier blanc, mesurant de préférence 21,5 sur 28 cm (8,5 sur 11 pouces), sur un côté de la page. Laissez toujours une marge d'au moins 2,5 cm.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Tout le manuscrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique.

En aucun endroit du manuscrit n'écrivez entièrement en majuscules.

Pour les références citées dans le texte, utilisez le système nom et année.

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude ?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons ? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou à l'intérieur du texte ? Est-ce que certaines données devraient être présentées séparément dans un rapport manuscrit ou dans un dépôt de données ?

Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la recherche ? Dans des énoncés de probabilité, seuls les tests statistiques sont-ils cités, et les tableaux statistiques inutiles sont-ils exclus ?

Le texte y gagnerait-il en clarté s'il plus condensé, en tout ou en partie ? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité ? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction ?

Le *titre* est-il représentatif du contenu du rapport ? Le *résumé donne-t-il l'essentiel des connaissances nouvelles ? L'introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude ? La revue de la littérature se limite-t-elle à la définition du problème ? La section *matériel et méthodes* contient-elle le minimum de détail qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données ? Les généralisations sur les *résultats* sont-elles adéquates ? Permettent-elles de distinguer entre constatations et déductions ? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes ?

Sont énumérés ci-dessous des façons d'éviter les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

1) Insérez la bande bibliographique avant le résumé (auteurs, date, titre, Can. J. Fish. Aquat. Sci.)

2) Limitez le résumé à un paragraphe d'environ 175 mots.

3) Dactylographiez à double interligne tous les éléments du manuscrit, y compris les références et les légendes des tableaux et des figures.

4) Évitez partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.

5) Ne soulignez que les noms latins d'organismes et certaines notations statistiques et mathématiques, qui devront être imprimés en italique.

6) Dans les figures, les tableaux et le texte, exprimez les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placez un zéro avant la virgule décimale.

7) Évitez les formes ambiguës, telles que g $C/m^2/d$; utilisez plutôt g $C \cdot m^{-2} \cdot d^{-1}$.

8) Identifiez le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire d'en donner la référence.

9) Dans le texte, généralisez à partir des tableaux et des figures ; évitez une répétition de tous les détails. Assurez-vous que tous les tableaux et figures sont indépendants et que, dans le texte, on y réfère dans l'ordre numérique. Les légendes doivent indiquer le but du tableau ou de la figure.

10) Préparez la section des remerciements au stade du manuscrit et non quand vous parviennent les épreuves.

11) En référant à des communications personnelles, donnez les initiales et l'adresse postale de la personne en cause.

12) Éliminez toutes références inutiles qui ne s'appliquent pas directement au problème.

13) Vérifiez soigneusement les références en regard des citations dans le texte et vice versa, afin de vous assurer qu'il y a correspondance. Dans le cas de matériel difficilement accessible, indiquez l'endroit où le trouver, p. ex., disponible auprès du Départment d'économique, Université Simon Fraser, Burnaby (C.-B.) V5A 1S6.

14) Éliminez les virgules entre le nom et la date dans les citations telles que (Smith 1900) et soulignez *et al*.

15) Dans les en-têtes de tableaux et les axes des figures, remplacez 10^n par les préfixes SI appropriés ou utilisez des mots en clair (p. ex. milliers).

16) Aux fins de la révision, les photocopies des figures, sauf les similis, sont appropriées. Sur demande, lorsqu'il s'agira de publier l'article, envoyez des photographies des figures, ou encore les originaux, s'ils ne dépassent pas 21,5 sur 38 cm. Utilisez autant que possible un lettrage uniforme.

Parties du manuscrit

Organisation

Organisez le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dressez une liste provisoire des sous-titres ou en-têtes, avec le moins de divisions possible. Retouchez-les jusqu'à ce qu'ils semblent assurer, pour le lecteur, une marche logique ; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'evaluer les résultats si vous décrivez méthodes, résultats et discussion dans des sections séparées.

Organisez les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. Assurez-vous que ces derniers sont aussi clairs que possible sans référence au texte.

Commencez les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particuliers. Si vous donnez d'abord une conclusion que vous appuyez ensuite, non seulement votre travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction des manuscrits, le défaut le plus commun est d'omettre de donner, au début, les généralités les plus dignes de mention.

Voyez à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger les paragraphes, composez la phrase-thème de chaque paragraphe et disposez ces phrases dans l'ordre approprié.

Titre

Limitez le titre à ce que le travail veut démontrer. C'est la clé de l'article, et il devrait montrer clairement et de façon concise ce qui est contenu dans le travail lui-même. Le titre a deux fonctions : 1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et 2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance possible de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, au besoin, la méthode d'approche technique (p. ex. rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que «Sur» ou «Vers», ou des expressions telles que «Contribution à . . .» ou «Recherches sur . . .». De bons titres facilitent le classement des publications et leur utilisation par les scientifiques et les bibliothécaires.

Résumé

Le résumé doit refléter succintement le contenu et les points principaux de l'article en 175 mots environ. Comme le titre, le résumé permet aux lecteurs de prendre connaissance du contenu de l'article et de décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquez au début du résumé la principale conclusion de l'étude et appuyez-la par des découvertes pertinentes. Ne donnez que les détails des méthodes nécessaires à la compréhension de ce qui a été fait et insérez-les dans l'énoncé des découvertes. Évitez l'emploi de phrases telles que «. . . on y analyse» ou «. . . a été trouvé» ; soyez spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et de classement, et que c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir, il est important que le résumé reflète précisément le contenu du travail.

Introduction

Limitez l'introduction à la portée, au but et à la raison de l'étude. Ne mentionnez que les travaux publiés et autres informations nécessaires à la définition du problème et à la perspective du travail. Commencez avec le but ou la portée du travail, définissez ensuite le problème et ajoutez ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375–500 mots.

Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limitez les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si vous présentez, autant que possible, toute l'information dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référez à ces publications et ne décrivez en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme : «Afin de déterminer . . . nous . . .» Si la section est longue, songez à utiliser des sous-titres correspondant à ceux que vous utilisez dans la section des résultats.

Résultats

Limitez les résultats aux réponses apportées aux questions en rapport avec le but de l'étude ; que ces réponses soient aussi complètes que possibles, tout en étant concises. Exprimez ce que vous avez trouvé, autant que possible dans les mêmes termes que ceux dans lesquels les observations ou les mesures ont été faites, évitant ainsi de confondre faits et spéculations. En dégageant les généralités des tableaux et des figures, référez-y et évitez de répéter dans le texte ce que les légendes devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans les séries des rapports ou dans un dépôt de données reconnu, et on y référera dans le texte.

Discussion

Limitez la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synthèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, notez-les et faites ressortir la manière dont vos résultats corroborent ou contredisent les travaux déjà publiés. Limitez la spéculation à ce que vous pouvez appuyer sur des preuves raisonnables. Terminez cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule et même section.

Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements aux personnes qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou amélioré la qualité de la présentation. Évitez de mentionner les personnes qui n'ont fourni qu'un travail de soutien.

Références

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux et communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (incluant les adresses). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'endroit où l'on peut se les procurer. On doit s'assurer que les références mentionnées dans le texte correspondent à celles qui sont contenues dans la liste de références et vice versa. Presque tous les manuscrits soumis au *Journal* contiennent des erreurs dans cette section.

Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible.

Agencez les tableaux de façon qu'ils s'adaptent soit à 1, 1½- ou 2 colonnes du *Journal*.

Dactylographiez chaque tableau sur une page séparée et numérotez-les en chiffres arabes.

Tracez des lignes horizontales de part et d'autre des en-têtes et au-dessous des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplementaires.

Chaque tableau doit avoir une légende instructive, complète et indépendante.

Les renvois des tableaux doivent être indiqués par des petites lettres suscrites dactylographiées au bas du tableau.

Placez les tableaux après la liste des références.

Quand on réfère à un tableau pour la première fois, on indique dans la marge du manuscrit «Tableau — près d'ici».

Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le corps du texte. Ils ont rarement besoin de lignes horizontales.

Figures

Fournissez des photographies ou les dessins originaux (pourvu qu'ils ne dépassent pas 21,5 sur 28 cm) de chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas sur l'illustration même. Transmettez deux photocopies des dessins au trait et deux séries de photos qui serviront au moment de la révision.

Les dessins devront occuper une largeur de 1, 1½- ou 2 colonnes du *Journal*. Assurez-vous que tous les chiffres, lettres et symboles sont lisibles, clairs et mesurent au moins 1,5 mm de hauteur une fois réduits. Les figures ne devraient pas être montées, brochées ou fixées à l'aide de trombones. Autant que possible, elle devraient être groupées et préparées avec le même type de lettrage.

Dactylographiez les légendes, dans l'ordre, sur des feuilles séparées. Dans le cas de cartes, photomicrographies, diagrammes d'instruments, etc., ajoutez une échelle.

À l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge «Fig. — près d'ici».

On devra autant que possible éviter les illustrations préparées par ordinateur, qui ne se reproduisent pas très bien. Les imprimantes par points ne peuvent produire de lignes solides suffisamment foncées pour être lisibles. On obtiendra toujours de meilleurs résultats en utilisant de l'encre de Chine noire. Si vous utilisez du lettrage instantané, veillez à ce qu'il adhère parfaitement.

Il vaut mieux dessiner que dactylographier les inscriptions relatives aux axes.

La production de planches en couleurs est très dispendieuse et on ne devrait utiliser celles-ci que lorsque les couleurs sont essentielles à la compréhension du texte. Les coûts supplémentaires de reproduction de planches en couleurs sont ordinairement débités à l'auteur. Pour les reproductions en couleurs, ne soumettez que des photos d'excellente qualité. Nous préférons utiliser des photographies en couleur, mais acceptons dessins, négatifs, diapositives ou positifs de films en couleurs.

Expressions, équations et formules mathématiques

Laissez trois espaces au-dessus et au-dessous des lignes portant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous des équations et des formules. Placez chaque composante des différentes expressions dans la position qui lui est propre.

Indiquez clairement tous les symboles. Épelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Appendice

Abréviations

N'abrégez les termes désignant les unités de poids et mesures dans la texte que lorsqu'ils sont précédés d'un nombre.

an	an
année	a
becquerel	Bq
calorie	cal
centimètre	cm
centimètre carré	cm^2
centimètre cube	cm^3
centimètre par gamme par seconde	$cm \cdot g^{-1} \cdot s^{-1}$
coulomb	C
décimètre	cm
degré Celsius	°C
degrés de liberté	dl
écart type	ET
élecronvolt	eV
erreur type	ErT
farad	F
gramme	g
hectare	ha
hertz	Hz
heure	h
joule	J
jour	d
kilomètre	km
litre	L
lumen	lm
lux	lx
mètre	m
mètre caré	m^2
mètre cube	m^3
micromètre	μm
milligramme	mg
millilitre	mL
millimètre	mm
millimètre carré	mm^2
minute	min
mois	mo
masse molaire	M
mole	mol
moles par litre	mol/L, M
pascal	Pa
seconde	s
semaine	sem
tonne	t
volt	V
volume	vol
watt	W

Dates

On écrira les dates dans l'ordre jour-mois-année, p.ex. 9 octobre 1983, sans virgule entre le mois et l'année.

Citations de références dans le texte

Système de nom et année

Le *Journal* utilise le système de nom et année, c.-à-d. que le nom de l'auteur ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié : «Brown (1983) compare . . .» ou «. . . on a comparé (Brown 1983)». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de «et al.» : «Brown et al. (1983) comparent . . .» ou «. . . on a comparé (Brown et al. 1983).»

Communications personnelles

Les communications personnelles ne doivent pas être incluses dans la liste des références. Utilisez plutôt des parenthèses dans le texte, entre lesquelles vous indiquerez le nom et l'adresse de la personne en question, suivis de «comm. pers».

Données inédites

Si le livre ou l'article inédits ont été acceptés pour publication, insérez-les dans la liste des références, avec la mention «(Sous presse)». On ne peut considérer comme étant sous presse que les manuscrits au stade d'épreuves ou ceux couverts par lettre d'acceptation. Si l'article a été soumis mais n'a pas encore été accepté, ne l'incluez pas dans la liste de références, mais indiquez le nom et l'adresse de l'auteur du matériel inédit, dans le texte lui-même, avec la mention «données inédites».

Liste de références

La liste qui suit donne des exemples de ponctuation, de style et d'abréviations utilisés dans les références bibliographiques (d'aprés les *Serial Sources for the BIOSIS Data Base*).

Article du journal

Archambault, D. et E. Bourget. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieu subarctique. Can. J. Fish. Aquat. Sci. 40: 1278–1292.

Numéro complet du journal

Gordon, D. C. Jr. et A. S. Hourston éd.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish Aquat. Sci. 40: (Suppl. 1): 1–365.

Livre dans une série

Hilton, J. W. et S. J. Slinger. 1981. Nutrition et alimentation de la truite arc-en-ciel. Publ. spéc. can. sci. halieut. aquat. 55 : 17 p.

Livre ne faisant pas partie d'une série

Forrester, W. D. 1983. Manuel canadien des marées. Ministère des Pêches et des Océans. Service hydrographique du Canada, Ottawa (Ont.) 148 p.

Partie d'un livre

Aubert, M., J. Aubert, S. Daniel et N. Desirotte. 1982. État actuel de la pollution bactérienne au large des côtes françaises, p. 36–40. *Dans* M. Ruivo [éd.] La pollution des mers et les ressources biologiques. Fishing News (Books) Ltd., Londres.

Corporation-auteur

American Public Health Association, American Water Works Association et Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14^{e} éd. Washington, DC. 1193 p.

Thèse

Delisle, C. 1969. Écologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la répartition en eau douce du Québec. Thèse doctorale, Univ. Ottawa, Ottawa (Ont.). 161 p.

Rapports

Dutil, D. J., M. Fortin et Y. Vigneault. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement du Québec. Rapp. manus. can. halieut. aquat 1653 : 29 p.

Traduction

Koike, A. et M. Ogura. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64: 1–11. (Traduit du japonais par Can. Transl. Fish Aquat. Sci. 4950, 1983)

Temps

On devra séparer par deux points (:) heures et minutes, et minutes et secondes. Les symboles «h,» «min» et «s» ne seront pas utilisés car ils représentent heure, minute et seconde dans le sens de durée ou intervalle de temps de douze heures et trente minutes, alors que 12:30 se rapporte à l'heure du jour.

Liste de mots

Cette section, dans la version anglaise du Guide, contient une série de mots dont l'orthographe pose certains problèmes d'uniformité, comme, par exemple, «cold water» (n.) «cold-water» (adj.); ‹hard water› (n.), «hardwater› (adj.), etc. L'auteur préparant une texte en anglais est prié de consulter la version anglaise du Guide.

Letters and Comments/Lettres et Commentaires

Mosegaard, H. What is reflected by otolith size at emergence? — a reevaluation of the results in West and Larkin (1987) 225–228
West, C. J., and P. A. Larkin. Reply to H. Mosegaard on "what is reflected by otolith size at emergence?" 228
Hayward, R. S. Comment on Boisclair and Leggett: can eating really stunt your growth? 228–230
Boisclair, D., and W. C. Leggett. On the relationship between growth and consumption rates: response to comments by R. S. Hayward (1989) 230–233

Announcement/Avis 234
Guide for Authors/Guide des auteurs *i–x*

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 47, No. 1, January 1990 **Volume 47, n° 1, janvier 1990**

J. C. Stevenson Memorial Lecture

Peterman, R. M. Statistical power analysis can improve fisheries research and management 2–15

Stockner, J. G., M. E. Klut, and W. P. Cochlan. Leaky filters: a warning to aquatic ecologists 16–23
Schnute, J. T., and L. J. Richards. A unified approach to the analysis of fish growth, maturity, and survivorship data 24–40
Ahlgren, M. O. Diet selection and the contribution of detritus to the diet of the juvenile white sucker (*Catostomus commersoni*) 41–48
Ahlgren, M. O. Nutritional significance of facultative detritivory to the juvenile white sucker (*Catostomus commersoni*) 49–54
Marmorek, D. R., M. L. Jones, C. K. Minns, and F. C. Elder. Assessing the potential extent of damage to inland lakes in eastern Canada due to acidic deposition. I. Development and evaluation of a simple "site" model 55–66
Jones, M. L., C. K. Minns, D. R. Marmorek, and F. C. Elder. Assessing the potential extent of damage to inland lakes in eastern Canada due to acidic deposition: II. Application of the regional model 67–80
Pike, D. G., and H. E. Welch. Spatial and temporal distribution of the sub-ice macrofauna in the Barrow Strait area, Northwest Territories 81–91
Benke, A. C., and J. B. Wallace. Wood dynamics in the Coastal Plain Blackwater streams 92–99
Wurtsbaugh, W. A., and T. S. Berry. Cascading effects of decreased salinity on the plankton, chemistry, and physics of the Great Salt Lake (Utah) 100–109
Pinel-Alloul, B., G. Méthot, G. Verreault, and Y. Vigneault. Zooplankton species associations in Quebec lakes: variation with abiotic factors, including natural and anthropogenic acidification 110–121
Eberhardt, L. L. A fur seal population model based on age structure data 122–127
Jackson, L. J., J. G. Stockner, and P. J. Harrison. Contribution of *Rhizosolenia eriensis* and *Cyclotella* spp. to the deep chlorophyll maximum of Sproat Lake, British Columbia, Canada 128–135
Kline, T. C. Jr., J. J. Goering, O. A. Mathisen, and P. H. Poe. Recycling of elements transported upstream by runs of Pacific salmon: I. δ^{15}N and δ^{13}C evidence in Sashin Creek, southeastern Alaska 136–144
Collie, J. S., R. M. Peterman, and C. J. Walters. Experimental harvest policies for a mixed-stock fishery: Fraser River sockeye salmon, *Oncorhynchus nerka* 145–155
James, W. F., R. H. Kennedy, and R. F. Gaugush. Effects of large-scale metalimnetic migration events on phosphorus dynamics in a north-temperate reservoir 156–162
Campana, S. E., K. C. T. Zwanenburg, and J. N. Smith. ^{210}Pb/^{226}Ra determination of longevity in redfish 163–165
Reinertsen, H., A. Jensen, J. I. Koksvik, A. Langeland, and Y. Olsen. Effects of fish removal on the limnetic ecosystem of a eutrophic lake 166–173
Noltie, D. B. Intrapopulation variation in the breeding of male pink salmon (*Oncorhynchus gorbuscha*) from a Lake Superior tributary 174–179
Madenjian, C. P. Nighttime pond respiration rate: oxygen or temperature dependent? 180–183
Sullivan, P. J., H.-L. Lai, and V. F. Gallucci. A catch-at-length analysis that incorporates a stochastic model of growth 184–198
Angradi, T. R., and J. S. Griffith. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho 199–209
Freda, J., and D. G. McDonald. Effects of aluminum on the leopard frog, *Rana pipiens:* life stage comparisons and aluminum uptake 210–216
Freda, J., V. Cavdek, and D. G. McDonald. Role of organic complexation in the toxicity of aluminum to *Rana pipiens* embryos and *Bufo americanus* tadpoles 217–224

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